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PLANKTONIC CNIDARIANS IN THE OPEN SOUTHERN ADRIATIC SEA: A COMPARISON OF HISTORICAL AND RECENT DATA

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ABSTRACT

This review compares historical data sets (1967–68, 1974–1976, 1993–1995) to the most recent data (2002–2004) on the composition, abundance, bathymetric distribution, and vertical migration of cnidarians of the deep southern Adriatic. 18 species of medusae are typical open-ocean holoplantonic species and 6 of these were either always or frequently found in samples, namely Rhabdoon singulare, Aglaura hemistoma, Persa incolorata, Rhopalonema velatum, Sminthea eurygaster, *and* Solmissus albescens. *The most common calycophore siphonophores are* Lensia subtilis, L. meteori, Eudoxoides spiralis, Sphaeronectes gracilis, *and* S. irregularis *followed by* Hippopodius hippopus, Vogtia penthacantha, Lensia conoidea, L. fowleri, Chelophyes appendiculata, Kephyes ovata, *and* Bassia bassensis. *Some differences in presence and abundance between historical and recent data are noted.*

Key words: South Adriatic, medusae, calycophoran siphonophores, composition, abundance, bathymetric distribution

CNIDARI PLANCTONICI IN ACQUE APERTE DELL'ADRIATICO MERIDIONALE: CONFRONTO FRA DATI STORICI E RECENTI

SINTESI

L'articolo confronta serie di dati storici (1967–68, 1974–1976, 1993–1995) con quelli più recenti (2002–2004) inerenti la composizione, l'abbondanza, la distribuzione batimetrica e la migrazione verticale dei cnidari delle acque profonde dell'Adriatico meridionale. 18 specie di meduse sono tipiche specie oloplanctoniche di acque aperte; 6 di queste sono state ritrovate sempre o molto frequentemente nei campioni. Si tratta di Rhabdoon singulare, Aglaura hemistoma, Persa incolorata, Rhopalonema velatum, Sminthea eurygaster, e Solmissus albescens. *I più comuni sifonofori calicofori sono* Lensia subtilis, L. meteori, Eudoxoides spiralis, Sphaeronectes gracilis *e* S. irregularis*, seguiti da* Hippopodius hippopus, Vogtia penthacantha, Lensia conoidea, L. fowleri, Chelophyes appendiculata, Kephyes ovata *e* Bassia bassensis. *Nell'articolo vengono presentate alcune differenze nella presenza e nell'abbondanza fra dati storici e recenti.*

Parole chiave: Adriatico meridionale, meduse, sifonofori calicofori, composizione, abbondanza, distribuzione batimetrica

INTRODUCTION

Planktonic cnidarians are an important and often conspicuous component of the top trophic level of many marine ecosystems. Knowledge of their spatial and temporal variability and their production dynamics is essential to understand the flow of energy and cycle of materials in these systems (Persad *et al.*, 2003).Owing to the comparative difficulties of open-ocean sampling, it is not surprising that relatively fewer observations of diversity and abundance have been reported for pelagic cnidarians and other pelagic gelatinous taxa than for those in more accessible nearshore waters (Youngbluth *et al.*, 2008).

The combination of over-fishing, eutrophication, climate change, translocation, and habitat modification that have been documented over the recent years in a wide range of marine areas appear to have favoured the development of jellyfish populations over that of other marine organisms (Molinero *et al.*, 2008; Richardson *et al.*, 2009). This upsurge of jellyfish was sufficiently dramatic and wide-spread that it attracted notable scientific and even popular attention (Purcell, 2005).

This same pattern has also been reported in the Adriatic Sea, but so far only for coastal waters. For example, previously unrecorded blooms of *Muggiea atlantica* was found in the northern Adriatic (Kršinić & Njire, 2001), the formerly dominant *M. kochi* was replaced by a congener, *M. atlantica*, in the eastern southern Adriatic, and schyphomedusae, especially *Pelagia noctiluca*, underwent unusually persistent blooms along the eastern Adriatic coast (Benović & Lučić, 2001; Miloš, 2009).

Research on planktonic cnidarians has a long tradition in the Adriatic Sea (see Benović & Lučić, 1996; Gamulin & Kršinić, 2000). The open southern Adriatic Sea is one of the few parts of the Mediterranean that has been subjected to relatively constant study of cnidarians over the past 70 years (Gamulin, 1966, 1968, 1977; Benović, 1973, 1976; Bender & Benović, 1986; Benović & Bender, 1987; Gamulin & Kršinić, 1993a,b, 2000; Benović & Lučić, 1996, 2001; Batistić *et al.*, 2004; Benović *et al.*, 2005, Lučić *et al*, 2005, 2009). Comparative analysis of data collected over this period is made easier by the similar sampling methodology used in all studies: that is, vertical tows in several specific layers with standard plankton nets. Although the presentation of results differs from paper to paper, certain useful indicators of system change, such as species composition, relative abundance, and bathymetric distribution, can be extracted from the published data.

Four comprehensive older publications were used in the current analysis: Benović (1976) describes the monthly distribution and abundance of hydromedusae from July 1967 to June 1968; Bender & Benović (1986) and Benović & Bender (1987) evaluate the distribution of medusae based on material collected during seasonal cruises from 1974 to 1976 at five stations in the deep southern Adriatic; Gamulin & Kršinić (2000) consolidate older data on calycophore siphonophores in the Adriatic Sea based on monthly sampling from July 1967 to June 1968, seasonal cruises from 1974 to 1976, and five cruises from 1993 to 1995.

Similar but more recent investigations began again in 2002 for the international cooperative project *"Medusa",* summarized by Benović *et al.* (2005) and Lučić *et al.* (2005) who described the bathymetric distribution of medusae and calycophoran siphonophorae during spring 2002, and Lučić *et al.* (2009) who reported on diel vertical migrations of medusae in July 2003. This review compares historical and recent data on cnidarians from the deep southern Adriatic, with unpublished data from February and October 2004 incorporated into the analysis.

MATERIAL AND METHODS

Study area

The Southern Adriatic Sea is a semicircular oligotrophic basin with depths to about 1200 m (Fig. 1). It is confluent with the Eastern Mediterranean Sea via inflow of Ionian Surface Water and Levantine Intermediate Water through the Strait of Otranto (~ 800 m depth), and

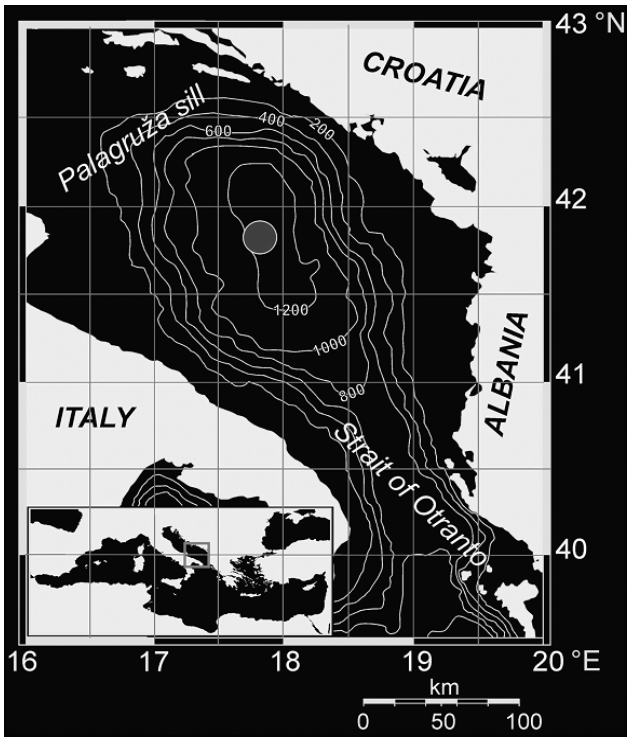

Fig. 1: Location of sampling in the southern Adriatic.
Sl. 1: Lokacija vzorčenja v južnem Jadranu.

with other regions of the Adriatic Sea via currents moving along the Adriatic coast. The region is a source of deep-water that participates in the broader circulation of the Mediterranean Sea (Vilibić & Orlić, 2001) and also features a cyclonic gyre that is present throughout the year (Gačić *et al.*, 2002). Each water mass has a characteristic species assemblage, and the above circulation patterns therefore play an important role in the spatial and seasonal distribution of small zooplankton of the southern Adriatic (Kršinić & Grbec, 2006).

The thermocline starts to form in May and is well developed at 14 m by July or August (Morović *et al.*, 2006). In the deepest layers, temperature is rather constant (from 13 to 15 ^{0}C) during the whole year. Salinity is generally higher than 38 throughout the water column (Morović *et al.*, 2006). In September and October, the thermocline is still relatively shallow, at 40 m. As in other parts of the Mediterranean, the thermocline disappears completely in late autumn and winter owing to vertical mixing driven by strong winds.

Whereas temperature changes in the upper 100 m are easily traced to seasonal influences of the local climate, those in deep layers are governed by inter-annual variations in circulation caused by larger-scale pressure differences (Grbec *et al.*, 2009). The deep Mediterranean water that passes through the Strait of Otranto is relatively warmer, saltier, and richer in nutrients than the typical southern Adriatic water. Nutrients often enhance planktonic productivity and, precisely phytoplankton blooms linked to these deeper water masses have been observed (Gačić *et al.*, 2002).

Material and methods

All data analyzed in this paper were collected in the deepest area of the southern Adriatic (1000–1200 m depth). Benović (1976) sampled monthly with an Indian Ocean standard closing net (250 µm mesh, 100 cm diameter) at 0–100, 100–200, 200–300, 300–400, 400–600, and 600–1000 m. Bender & Benović (1986) and Benović & Bender (1987) used the same nets but sampled with vertical hauls from bottom to surface. The same methodologies were used to collect samples for description of calycophorans during the same period (Gamulin & Kršinić, 2000); from 1993–1995 samples were collected at 0–50, 50–100, 100–200, 300–400, 400–600, and 600–1000 m (Tab. 1).

Project *"Medusa"* used Nansen opening-closing nets (200 µm mesh, 113-cm diameter) within the following layers: 0–50, 50–100, 100–200, 300–400, 400–600, 600–800, 800–1200 m. The most extensive sampling was conducted in July 2003 when nineteen series (152 vertical hauls) were collected. Owing to a strong thermocline at about 15 m, samples were taken from 0–15 m (above the thermocline) and from 15–50 m depth. Benović *et al.* (2005) and Lučić *et al.* (2005, 2009) provide a detailed description of the study area, sampling program, and methodology for spring and summer cruises. The same methodology was used in February and October 2004 (unpubl. data) when six (48 hauls) and three (24 hauls) sample series, respectively, were collected (Tab. 1).

All plankton samples were preserved in 2.5% formalin-sea water solution buffered with $CaCO_3$. Cnidarians were identified with a stereomicroscope. Results from historical investigations were presented as the total number of specimens (Benović, 1976; Benović & Bender, 1987) or number of individuals per m^2 (Bender & Benović, 1986; Gamulin & Kršinić, 2000). Medusae and calycophoran nectophores (polygastric only) in the recent work are expressed as the number of individuals per m^3 or 10 m^3. Because of these differences, historical and recent comparisons are based on relative frequency of occurrence and abundance where relative frequency of occurrence is: r = rare, observed in < 10% samples during the sampling period; f = frequent, observed in 10%–50% samples during the sampling period; vf = very frequent, observed in >50% during the sampling period.

Tab. 1: Historical and recent arrangement of sampling methodology in the Southern Adriatic Sea.
Tab. 1: Pregled pretekle in sedanje metodologije vzorčenja v južnem Jadranskem morju.

Sampling years	Methodology of sampling	Depth layers (m)
1967–1968	Indian Ocean standard closing net, 100 cm diameter, 250 cm long, mesh size 250 µm	100–0, 200–100, 300–200, 400–300, 600–400, 1000–600
1974–1976	Indian Ocean standard closing net, 113 cm diameter, mesh size 250 µm	From bottom to surface
1993–1995	Nansen opening-closing net, 113 cm diameter, 350 cm long, mesh size 250 µm	50–0, 100–50, 200–100, 300–200, 400–300, 600–400, 1000–600
2002–2004	Nansen opening-closing net, 113 cm diameter, 350 cm long, mesh size 200 µm	15–0, 50–15, 100–50, 200–100, 400–200, 600–400, 800–600, 1200–800

RESULTS AND DISSCUSION

Medusan frequency of occurrence

Most of the 55 medusan species that have been identified in the Adriatic Sea (Benović & Lučić, 1996) have a bentho-pelagic metagenetic life cycle and are carried to the open southern Adriatic with water currents. 18 species of medusae are typical open-ocean holoplantonic species (Tab. 2), 6 of which were always – or frequently – found in the Adriatic Sea: *Rhabdoon singulare*, *Aglaura hemistoma*, *Persa incolorata*, *Rhopalonema velatum*, *Sminthea eurygaster*, and *Solmissus albescens*. 3 – *Bythotiaria murrayi*, *Krampella dubia*, and *Haliscera bigelowi* – were rare. The frequency of occurrence of *Solmundella bitentaculata* and *Paraphyllina intermedia* appears to be seasonal. The bathypelagic trachymedusan *Haliscera bigelowi* and the coastal anthomedusan *Dicodonium adriaticum* were found only in recent investigations (Benović *et al.*, 2005).

Other differences between historical and recent data are worthy of note. For example, *Liriope tetraphylla*, traditionally among the most frequently encountered hydromedusae in this region, was collected only very rarely in recent investigations. In fact, the last time that this medusa was found frequently in samples from the southern Adriatic was November 1993 (Benović & Lučić, 1996). *L. tetraphylla* was observed to undergo large inter-annual variations in abundance and seasonality in the northwestern Mediterranean Sea, but these variations do not appear to be linked to long-term changes in hydrographic conditions (Buecher *et al.*, 1997). There was, however, an inverse relationship between the numbers of *L. tetraphylla* and the schyphomedusn *Pelagia noctiluca* (Buecher *et al.*, 1997). A mass occurrence of *P. noctiluca* observed in the Adriatic from 1997 to 2006 (unpubl. data) coincided with a drastic decrease of *L. tetraphylla* abundance. *Oceania armata*, *Amphinema rubra*, *Leuckartiara octona*, *Octophialucium funerarium*, and *Arctopodema australis* are now found more frequently than in previous investigations and may be considered characteristic of the open southern Adriatic. *Rhopalonema funerarium*, on the other hand, has been found only in recent investigations.

Tab. 2: List of typical Southern Adriatic Sea medusae collected from 1967 to 2004 and their relative frequency of occurrence: r = rare; f = frequent; vf = very frequent. Data sources: 1967–1968, Benović (1976); 1974–1976, Bender & Benović (1986) and Benović & Bender (1987); May 2002, Benović** et al. **(2005); July 2003, Lučić** et al. **(2009); February and October 2004, unpubl.

Tab. 2: Seznam tipičnih meduz južnega Jadranskega morja, zbranih od 1967 do 2004 in relativna pogostost njihovega pojavljanja: r = redko; f = pogosto; vf = zelo pogosto. Podatkovni viri: 1967–1968, Benović (1976); 1974–1976, Bender & Benović (1986) in Benović & Bender (1987); maj 2002, Benović** et al. **(2005); julij 2003, Lučić** et al. **(2009); februar in oktober 2004, neobjavljeno.

Species	1967–1968	1974–1976	May 2002	July 2003	Feb 2004	Oct 2004
Rhabdoon singulare	vf	vf	vf	vf	vf	f
Oceania armata		r	f	f	f	r
Amphinema rubra		r	vf	vf	vf	f
Leuckartiara octona		r	r	f	f	
Bythotiara murrayi	r	r		r		
Krampella dubia		r		r		
Octophialucium funerarium	r	r	r	vf	vf	
Haliscera bigelowi			r	r		
Liriope tetraphylla	vf	vf		r		
Aglaura hemistoma	vf	vf	vf	vf	vf	f
Arctapodema australis		r	f	vf	vf	f
Persa incolorata	vf	vf	vf	vf	vf	vf
Rhopalonema funerarium			r	r	f	r
Rhopalonema velatum	vf	vf	vf	vf	vf	vf
Sminthea eurygaster	vf	f	f	f	f	r
Solmundella bitentaculata	f	vf	f	f	f	
Solmissus albescens	vf	vf	vf	vf	vf	vf
Paraphyllina intermedia			f	f		

One obvious difference between historical and recent data is the presence of coastal species in the surface waters of the open southern Adriatic. Hydromedusae of the genera *Hydractinia*, *Boungainvillia*, *Clytia*, and *Obelia*, previously encountered very frequently, are now found only very rarely. This might be related to the substantial changes in the Anthomedusan and Leptomedusan fauna that have occurred in the northern Adriatic (Benović *et al.*, 1987). Namely, as the majority of these meta-genetic species has disappeared in the north, they are no longer transported along the Italian coast to populate the southern Adriatic fauna (Benović *et al.*, 2000).

Calycophoran frequency of occurrence

23 calycophore species were recorded, all in the southern Adriatic. Except for *Muggiaea kochi* and *M. atlantica*, all of these species are common to, or exclusively found in, the open sea. Compared with historical data, only the rarely encountered *Rosacea cymbiformis* and *Sulculeolaria quadrivalvis* were not found in thee recent work.

Calycophore frequency of occurrence does not differ substantially in historical and recent data (Tab. 3). The southern Adriatic's well-developed cyclonic gyre (Gačić *et al.*, 2002) probably contributes to maintaining a relatively constant composition of the plankton community, including gelatinous taxa. The most common species are *Lensia subtilis*, *L. meteori*, *Eudoxoides spiralis*, *Sphaeronectes gracilis*, and *S. irregularis*, followed by *Hippopodius hippopus*, *Vogtia penthacantha*, *L. conoidea*, *L. fowleri*, *Chelophyes appendiculata*, *Kephyes ovata*, and *Bassia bassensis*. The calycophoran *K. ovata*, previously known as *Clausophyes ovata*, was reclassified by Pugh (2006).

Tab. 3: List of typical Southern Adriatic Sea calycophoran nectophores collected from 1965 to 2004 and their relative frequency of occurrence: r = rare; f = frequent; vf = very frequent. Data sources: 1965–1994, summarized in Gamulin & Kršinić (2000); May 2002, Lučić** et al. **(2005); July 2003, Lučić** et al. **(2009); February and October 2004, unpubl.

Tab. 3: Seznam tipičnih kalikofornih cevkašev južnega Jadranskega morja, zbranih od 1965 do 2004 in relativna pogostost njihovega pojavljanja: r = redko; f = pogosto; vf = zelo pogosto. Podatkovni viri: 1965–1994, povzeto v Gamulin & Kršinić (2000); maj 2002, Lučić** et al. **(2005); julij 2003, Lučić** et al. **(2009); februar in oktober 2004, neobjavljeno.

Species	1965–1994	May 2002	July 2003	Feb 2004	Oct 2004
Rosacea cymbiformis	r				
Hippopodius hippopus	f	f	r	f	
Vogtia pentacantha	r	r	f	f	r
Sulculeolaria quadrivalvis	r				
Sulculeolaria turgida	r				
Sulculeolaria chuni	r	r	r		
Diphyes dispar	r				
Lensia conoidea	f	f	f	f	r
Lensia multicristata	r	r	r		
Lensia fowleri	r	f	f	f	
Lensia subtilis	vf	vf	vf	vf	vf
Lensia campanella	r	r	r		
Lensia meteori	vf	vf	vf	vf	vf
Lensia subtiloides	r		r		
Chelophyes appendiculata	f	r	r	f	f
Eudoxoides spiralis	vf	vf	vf	f	vf
Sphaeronectes gracilis	f	vf	vf	vf	
Sphaeronectes irregularis	vf	f	vf	vf	f
Sphaeronectes gamulini	r	r			
Sphaeronectes fragilis	r	r	r		
Kephyes ovata	r	f	f	f	r
Abylopsis tetragona	f	r	r		
Bassia bassensis	f	r	f	f	r

Medusan abundance

These data suggest that important changes have occurred in medusan abundance. Total abundance appears to be higher in recent studies. This is especially the case for *Rhabdoon singulare*, *Oceania armata*, *Octophialucium funerarium*, and *Arctapodema australis*. These species were historically relatively rare, but they are decidedly more abundant and sometimes dominant in our more recent samples (Tab. 4). On the other hand, *Liriope tetraphylla*, previously one of the more numerous medusae, has undergone a dramatic decrease, and in some cases it was absent altogether. *Aglaura hemistoma*, *Persa incolorata*, *Rhopalonema velatum*, and *Solmissus albescens*, however, have remained regularly abundant.

The massive appearance of meroplanktonic coastal species that occurred seasonally in historical studies has not been observed in our more recent work. Nevertheless, medusan densities above 100 m in May 2002 and July 2003 are among the highest reported for any open-sea environment (see Benović *et al.*, 2005 and Lučić *et al.*, 2009). For example, particularly high densities of *Rhopalonema velatum* were found in the 50–100 m layer, with 358 ind. 10 m^{-3} in May 2002, 93 ind. 10 m^{-3} in July 2003, and 51 ind. 10 m^{-3} in February and October 2004.

Calycophoran abundance

There was no detectable change in the abundance of calycophoran species between earlier and recent samples. *Lensia subtilis* continues to be the most numerous species, followed by *Eudoxoides spiralis* and *L. meteori*. *Sphaeronectes gracilis* and *S. irregularis* also were abundant.

Several species do, however, appear at notably higher abundance in recent investigations (Tab. 5). In particular, *Kephyes ovata* was more numerous; in July 2003, there was an unusually high number of *Vogtia pentacantha*. Further, one of the highest nectophore densities yet reported for the open sea (275 nectophores 10 m^{-3}) was found above 50 m at night in May 2002, due primarily to *L. subtilis* (Lučić *et al.*, 2005).

Tab. 4: Relative abundance of Southern Adriatic Sea medusae collected from 1967 to 2004. Historical data were recalculated as number of individuals per 10 m^3: + = <1 ind. 10 m^3; c = 1–5 ind. 10 m^3; cc = >5–10 ind. 10 m^3; ccc = >10 ind. 10 m^3. Data sources: 1967–1968, Benović (1976); 1974–1976, Bender & Benović (1986) and Benović & Bender (1987); May 2002, Benović** et al. **(2005); July 2003, Lučić** et al. **(2009); February and October 2004, unpubl.

Tab. 4: Relativna številčnost meduz južnega Jadranskega morja, zbranih od 1967 do 2004. Podatki iz preteklih študij so bili preračunani na število osebkov na 10 m^3: + = <1 ind. 10 m^3; c = 1–5 ind. 10 m^3; cc = >5–10 ind. 10 m^3; ccc = >10 ind. 10 m^3. Podatkovni viri: 1967–1968, Benović (1976); 1974–1976, Bender & Benović (1986) in Benović & Bender (1987); maj 2002, Benović** et al. **(2005); julij 2003, Lučić** et al. **(2009); februar in oktober 2004, neobjavljeno.

Species	1967–1968	1974–1976	May 2002	July 2003	Feb 2004	Oct 2004
Rhabdoon singulare	c	c	ccc	ccc	c	c
Oceania armata		+	c	c	cc	c
Amphinema rubra		+	c	cc	c	+
Leuckartiara octona		+	+	c	+	
Bythotiara murrayi	+	+		+		
Krampella dubia		+		+		
Octophialucium funerarium	+	+	+	c	c	
Haliscera bigelowi			+	+		
Liriope tetraphylla	ccc	ccc		+		
Aglaura hemistoma	ccc	ccc	c	ccc	ccc	c
Arctapodema australis		+	+	c	c	+
Persa incolorata	ccc	cc	cc	cc	ccc	c
Rhopalonema funerarium			+	+	+	+
Rhopalonema velatum	ccc	ccc	ccc	ccc	ccc	ccc
Sminthea eurygaster	cc	+	c	c	+	+
Solmundella bitentaculata	+	cc	c	c	c	
Solmissus albescens	cc	c	cc	ccc	ccc	c
Paraphyllina intermedia			+	+		

Tab. 5: Relative abundance of Southern Adriatic Sea calycophoran nectophores collected from1965 to 2004. Historical data were recalculated as number of nectophores per 10 m^3: + = <1 ind. 10 m^3; c = 1–5 ind. 10 m^3; cc = >5–10 ind. 10 m^3; ccc = >10 ind. 10 m^3. Data sources: 1965–1994, summarized in Gamulin & Kršinić (2000); May 2002, Lučić** et al. **(2005); July 2003, Lučić** et al. **(2009); February and October 2004, unpubl.
Tab. 5: Relativna številčnost kalikofornih cevkašev južnega Jadranskega morja, zbranih od 1965 do 2004. Podatki iz preteklih študij so bili preračunani na število nektoforov na 10 m^3: + = <1 ind. 10 m^3; c = 1–5 ind. 10 m^3; cc = >5–10 ind. 10 m^3; ccc = >10 ind. 10 m^3. Podatkovni viri: 1965–1994, povzeto v Gamulin & Kršinić (2000); maj 2002, Lučić** et al. **(2005); julij 2003, Lučić** et al. **(2009); februar in oktober 2004, neobjavljeno.

Species	1965–1994	May 2002	July 2003	Feb 2004	Oct 2004
Rosacea cymbiformis	+				
Hippopodius hippopus	c	c	+	c	
Vogtia pentacantha	+	+	cc	+	+
Sulculeolaria quadrivalvis	+				
Sulculeolaria turgida	+				
Sulculeolaria chuni	+	+	+		
Diphyes dispar	+				
Lensia conoidea	+	c	c	+	+
Lensia multicristata	+	+	+		
Lensia fowleri	+	+	c	+	
Lensia subtilis	ccc	ccc	ccc	ccc	ccc
Lensia campanella	+	+	+		
Lensia meteori	ccc	ccc	ccc	ccc	ccc
Lensia subtiloides	+		+		
Chelophyes appendiculata	c	+	+	c	c
Eudoxoides spiralis	cc	ccc	ccc	c	ccc
Sphaeronectes gracilis	c	ccc	ccc	cc	
Sphaeronectes irregularis	cc	c	cc	cc	c
Sphaeronectes gamulini	+	+			
Sphaeronectes fragilis	+	+	+		
Kephyes ovata	+	c	c	c	+
Abylopsis tetragona	c	+	+		
Bassia bassensis	c	+	c	c	+

There are several potential explanations for the increased abundance of planktonic cnidarians in recent samples:

a. Higher average water temperatures than in previous years (Gačić *et al.*, 2006) could have stimulated an increase in general plankton production. Accordingly, recent investigations found particularly high micro- and mesozooplankton densities (except in October 2004, when the total number of cnidarians was low).
b. Unlike previously, our recent investigations emphasized day-night sampling, with higher densities near the surface at night.
c. The short-term, repetitive sampling used in our recent work provides a more thorough temporal coverage of the study area and so it can be expected to characterize abundance more reliably and also capture less abundant components.

Medusan bathymetric distribution and vertical migration

As noted above, full understanding of the role of planktonic cnidarians in pelagic food webs requires knowledge of bathymetric distribution and migration patterns. Of many factors proposed to explain vertical migratory behavior, most attention was given to light intensity, hydrographic variables, feeding, and predator avoidance. Medusan vertical distributions and migration in the southern Adriatic have been described in recent papers (see Lučić *et al.*, 2009), except for *Solmissus albescens* (Benović, 1973). Table 6 summarizes these data.

Tab. 6: Seasonal bathymetric distribution of typical Southern Adriatic Sea medusae. Data sources only from recent investigations (2002–2004).
Tab. 6: Sezonska batimetrijska distribucija tipičnih meduz južnega Jadranskega morja. Podatkovni viri: samo novejše raziskave (2002–2004).

Species	Winter	Spring	Summer	Autumn
Rhabdoon singulare	0–200	50–600	15–600	50–200
Oceania armata	0–100	0–600	15–200	30–400
Amphinema rubra	15–400	100–600	100–800	100–200
Leuckartiara octona		50–400	50–600	
Bythotiara murrayi			200–400	
Krampella dubia			400–600	
Octophialucium funerarium	400–1200	200–800	200–1200	
Haliscera bigelowi		600–800	600–800	
Liriope tetraphylla		0–100	0–15	
Aglaura hemistoma	0–100	0–100	0–100	0–30
Arctapodema australis	200–1200	200–800	200–1200	400–800
Persa incolorata	0–1200	100–800	50–1200	0–600
Rhopalonema funerarium	400–1200	200–600	600–800	400–1200
Rhopalonema velatum	0–600	0–1200	0–800	0–600
Sminthea eurygaster	50–400	50–600	100–1200	
Solmundella bitentaculata	0–200	0–400	15–400	
Solmissus albescens	0–1200	0–1200	15–1200	50–1200
Paraphyllina intermedia		600–1200	400–1200	

The only pelagic cnidarian found exclusively above 100 m was *Aglaura hemistoma*, an omnivore that feeds on microphytoplankton and protists (Colin *et al.,* 2003). Most *A. hemistoma* occur quite near the surface, except during summer months when it aggregates just above the thermocline. *Liripe tertraphylla* is also a surface species.

Rhopalonema velatum, *Rhabdoon singulare*, and *Oceania armata* are sub-surface species found mainly above 100 m. These medusae rarely breached the thermocline, but during winter months they were sometimes abundant near the surface at night. Part of the *R. velatum* and *R. singulare* populations, however, sought deeper layers at night.

The more frequent and abundant medusae are characteristic members of the southern Adriatic's upper mesopelagic fauna. These are: *Amphinema rubra*, *Persa incolorata*, *Leuckartia octona*, *Sminthea eurygaster*, and *Solmundella bitentaculata,* as well as the rare species *Bythotiaria murrayi*. The highest frequency of occurrence and population density of these species is between 100 and 400 m. A common behavioral feature of this group is that they migrate in both directions at night, that is, both toward the surface and toward the bottom. Their vertical movements are also seasonal, such that in winter these species swim to the surface at night whereas at other times of the year they do not migrate shallower than 100 m depth.

Characteristic species of the lower mesopelagic are *Octophialucium funerarium*, *Arctapodema australis*, *Rhopalonema velatum,* and a very rare *Krampella dubia*. These species undergo extensive vertical migrations, with their upper border being 200 m.

The scyphomedusa *Paraphyllina intermedia* is mostly bathypelagic and migrates to within 400 m of the surface at night.

The most important vertical migrant is *Sollmisus albescens*, behaviorally distinguished from all other species: it has the widest vertical distribution and undertakes the most extensive diel migration, spanning more than 800 m at the average speed of 222 m/h (K. Katja Yong, *pers. comm.*). It aggregates within 400–800 m layer at midday and toward evening moves to upper layers. The highest abundance was found at night between the surface and 50 m. An exception to this pattern occurs in summer and autumn when its upward movement is blocked by a well-developed thermocline. *S. albescens* primarily eats other gelatinous organisms (Raskoff, 2002). Thus, its extensive migrations to surface layers might be explained by appreciably higher densities of their potential prey above 100 m at night.

Calycophoran bathymetric distribution and vertical migrations

There was substantial variation in the depth range of most common calycophorans (Tab. 7): *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 *Sphaeronectes gracilis* (0–200).

The species distributed mainly above 100 m depth were *Hippopodius hippopus*, *Lensia subtilis*, *L. campanula*, *Chelophyes appendiculata*, *Eudoxoides spiralis*, *Sphaeronectes gracilis*, *S. irregularis*, *S. gamulini*, and *Bassia bassensis*. Typical nocturnal movements toward the surface were recorded only for *L. subtilis* and *Sphaeronectes gracilis*, both of which aggregated below the thermocline during summer. *E. spiralis* migrated both toward the surface and below 100 m.

Calycophores found mainly below 100 m depth were *Sulculeolaria chuni*, *Lensia multicristata*, *L. fowleri*, *L. meteori*, *L. subtiloides*, and *Sphaeronectes fragilis*. These species migrated to shallower layers primarily in winter, except for *L meteori*, which was collected near the surface. Most specimens of *L. conoidea* and *Vogtia penthacantha* were collected below 400 m during the day but were as shallow as 100 m at night. *K. ovata* appears to be non-migratory.

There are some differences between historical (Gamulin & Kršinić, 2000) and recent data regarding the maximum depth of some calycophores. In particular, *V. penthacantha* was described earlier as a typical deep-sea species, but our recent collections show that it is routinely found as shallow as 100 m at night. These seeming historical differences are clearly a function of nighttime samples that characterize our more recent field work. Additionally, the maximum depth earlier reported for *Hippopodius hippopus*, *Lensia subtilis*, *L. campanulla*, and *Chelophyes appendiculata* was 1000 m, but this is not substantiated by recent investigations.

CONCLUSIONS

The present work reports historical and recent data on the species composition, abundance, bathymetric distribution, and vertical migrations of planktonic cnidarians in the water column over the deepest area of the oligotrophic South Adriatic Sea. 11 species were found on all cruises, with the more abundant being medusa *Rhopalonema velatum* and the siphonophore *Lensia subtilis*.

Tab. 7: Seasonal bathymetric distribution of typical Southern Adriatic Sea open-sea calycophores. Data sources from recent investigations (2002–2004).
Tab. 7: Sezonska batimetrijska distribucija tipičnih, v odprtih vodah južnega Jadranskega morja živečih kalikofornih cevkašev. Podatkovni viri: novejše raziskave (2002–2004).

Species	Winter	Spring	Summer	Autumn
Hippopodius hippopus	0–200	0–100	0–200	
Vogtia pentacantha	0–800	100–200	200–1200	400–600
Sulculeolaria chuni		100–400	0–200	
Lensia conoidea	100–1200	400–1200	100–1200	400–600
Lensia multicristata		100–400	100–400	
Lensia fowleri	50–400	100–400	100–600	
Lensia subtilis	0–600	0–200	0–600	0–200
Lensia campanella		50–100	50–400	
Lensia meteori	0–400	50–800	100–600	200–600
Lensia subtiloides			100–600	
Chelophyes appendiculata	0–200	0–100	15–50	200–600
Eudoxoides spiralis	0–200	0–300	0–1200	0–800
Sphaeronectes gracilis	0–200	0–400	0–200	
Sphaeronectes irregularis	0–600	50–200	15–600	50–400
Sphaeronectes gamulini		50–100		
Sphaeronectes fragilis		100–400	15–800	
Kephyes ovata	600–1200	600–1200	600–1200	
Abylopsis tetragona		100–400	0–50	
Bassia bassensis	0–100	0–100	0–200	0–50

Liriope tetraphylla, formerly among the most frequently encountered hydromedusae in the southern Adriatic, has become rare or absent in recent samples. On the other hand, *Oceania armata*, *Amphinema rubra*, *Leuckartiara octona*, *Octophialucium funerarium*, and *Arctopodema australis*, are now far more abundant than before. These 5 species are now quite common members of the open southern Adriatic planktonic ecosystem. With the exception of *O. armata*, all of these species are characteristic of mid-depth and bathypelagic layers.

One obvious difference between historical and recent collections is the presence of coastal species in the surface waters of the open southern Adriatic. Hydromedusae of the genera *Hydractinia*, *Boungainvillia*, *Clytia*, and *Obelia* that were frequently encountered in our older zooplankton samples are now quite rare. There is, however, no substantial difference in the frequency of occurrence of calycophores between historical and recent samples.

There is, nonetheless, an indication that cnidarians are generally more abundant in our more recently collected samples. This is especially the case for *Rhabdoon singulare*, *Oceania armata*, *Octophialucium funerarium*, and *Arctapodema australis*, species that were previously present only in low abundance and are now more abundant or, in some cases, even dominant. Higher abundances were recorded for other species during recent investigations, too. This could be explained by the increase of average temperature in the last decade and its influence on the general increase of plankton abundance, or it may be a sampling artifact associated with more frequent sampling at night.

The most common species migrated over a substantial depth range, presumably due to daily changes of irradiance and feeding biology. Higher surface layers temperature appeared to be an effective upper barrier for many cnidarians, especially mesopelagic species. Some populations performed migrations that appeared to track light intensity preference. Certain species also characterize given depth ranges. Long-term sampling programs are critical for an understanding of the planktonic species assemblages in the water column.

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PLANKTONSKI OŽIGALKARJI V ODPRTIH VODAH JUŽNEGA JADRANSKEGA MORJA: PRIMERJAVA PODATKOV IZ PRETEKLIH IN NOVEJŠIH RAZISKAV

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POVZETEK

V pričujočem članku avtorji primerjajo podatke iz preteklih (1967–68, 1974–1976, 1993–1995) in novejših raziskav (2002–2004), in sicer o zgradbi, številčnosti, batimetrijski distribuciji in vertikalni migraciji ožigalkarjev v globokih vodah južnega Jadrana. 18 vrst meduz je tipičnih holoplantonskih vrst, živečih v odprtih morjih; vzorci so vedno ali pogosto vsebovali 6 od teh, in sicer Rhabdoon singulare, Aglaura hemistoma, Persa incolorata, Rhopalonema velatum, Sminthea eurygaster *in* Solmissus albescens*. Najpogostejši kalikoforni cevkaši so* Lensia subtilis, L.

meteori, Eudoxoides spiralis, Sphaeronectes gracilis *in* S. irregularis *ter* Hippopodius hippopus, Vogtia penthacantha, Lensia conoidea, L. fowleri, Chelophyes appendiculata, Kephyes ovata *in* Bassia bassensis. *Pri primerjanju podatkov iz preteklih in novejših raziskav so bile ugotovljene nekatere razlike v prisotnosti in številčnosti.*

Ključne besede: južno Jadransko morje, meduze, kalikoforni cevkaši, zgradba, številčnost, batimetrijska distribucija

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