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VSEBINA / INDICE GENERALE / CONTENTS

BIOTSKA GLOBALIZACIJA
GLOBALIZZAZIONE BIOTICA
BIOTIC GLOBALIZATION**Murat BILECENOĞLU & M. Baki YOKEŞ**

New Data on the Occurrence of Two Lessepsian Marine Heterobranchs, *Plocamopherus ocellatus* (Nudibranchia: Polyceridae) and *Lamprohaminoea ovalis* (Cephalaspidea: Haminoeidae), from the Aegean Sea 267
 Novi podatki o pojavljanju dveh lesepskih morskih polžev zaškrjarjev, *Plocamopherus ocellatus* (Nudibranchia: Polyceridae) in *Lamprohaminoea ovalis* (Cephalaspidea: Haminoeidae), iz Egejskega morja

Gianni INSACCO, Aniello AMATO, Bruno ZAVA & Maria CORSINI-FOKA

Additional Capture of *Halosaurus ovenii* (Actinopterygii: Notacanthiformes: Halosauridae) in Italian Waters 273
 Novi ulov vrste *Halosaurus ovenii* (Actinopterygii: Notacanthiformes: Halosauridae) v italijanskih vodah

Christian CAPAPÉ, Christian REYNAUD & Farid HEMIDA

First Record of Marbled Stingray, *Dasyatis marmorata* (Chondrichthyes: Dasyatidae) from the Algerian Coast (Southwestern Mediterranean Sea) 281
 Prvi zapis o pojavljanju marmoriranega morskega biča, *Dasyatis marmorata* (Chondrichthyes: Dasyatidae) iz alžirske obale (jugozahodno Sredozemsko morje)

Maria CORSINI-FOKA & Bruno ZAVA

Second Occurrence of *Siganus javus* (Siganidae) in the Mediterranean Waters 287
 Drugi zapis o pojavljanju progastega morskega kunca, *Siganus javus* (Siganidae), v sredozemskih vodah

Daniel GOLANI, Haim SHOHAT & Brenda APPELBAUM-GOLANI

Colonisation of Exotic Fish Species of the Genera *Pseudotropheus* and *Aulonocara* (Perciformes: Cichlidae) and the Decline of Native Ichthyofauna in Nahal Amal, Israel 293
 Naseljevanje eksotičnih vrst rib iz rodov *Pseudotropheus* in *Aulonocara* (Perciformes: Cichlidae) in upad domorodne ribje favne v reki Nahal Amal, Izrael

Panayotis OVALIS & Maria CORSINI-FOKA

On the Occurrence of *Velolambrus expansus* (Brachyura, Parthenopidae) in Hellenic Waters 301
 O pojavljanju rakovice vrste *Velolambrus expansus* (Brachyura, Parthenopidae) v grških vodah

Saul CIRIACO, Marco SEGARICH, Vera CIRINÀ & Lovrenc LIPEJ

First Record of the Long-Jawed Squirrelfish *Holocentrus adscensionis* (Osbeck, 1765) in the Adriatic Sea 309
 Prvi zapis o pojavljanju vrste veveričjaka *Holocentrus adscensionis* (Osbeck, 1765) v Jadranskem morju

Christian CAPAPÉ, Vienna HAMMOUD, Aola FANDI & Malek ALI

First Record of Moontail Bullseye *Priacanthus hamrur* (Osteichthyes, Priacanthidae) from the Syrian Coast (Eastern Mediterranean Sea) 317
 Prvi zapis o pojavljanju lunastorepega velikookega ostriža *Priacanthus hamrur* (Osteichthyes, Priacanthidae) s sirske obale (vzhodno Sredozemsko morje)

SREDOZEMSKI MORSKI PSI
SQUALI MEDITERRANEI
MEDITERRANEAN SHARKS**Hakan KABASAKAL, Erdi BAYRI & Görkem ALKAN**

Distribution and Status of the Great White Shark, *Carcharodon carcharias*, in Turkish Waters: a Review and New Records 325
 Status in razširjenost belega morskega volka (*Carcharodon carcharias*) v turških vodah: pregled in novi zapisi o pojavljanju

Alen SOLDI

200 Years of Records of the Basking Shark, *Cetorhinus maximus*, in the Eastern Adriatic 343
 Dvesto let opazovanj morskega psa orjaka, *Cetorhinus maximus*, v vzhodnem Jadranskem morju

Hakan KABASAKAL, Ayşe ORUÇ, Cansu LKILINÇ, Efe SEVİM, Ebrucan KALECİK & Nilüfer ARAÇ

Morphometrics of an Incidentally Captured Little Gulper Shark, *Centrophorus uyato* (Squaliformes: Centrophoridae), from the Gulf of Antalya, with Notes on Its Biology 351
 Morfometrija naključno ujetega globinskega trneža, *Centrophorus uyato* (Squaliformes: Centrophoridae), iz Antalijskega zaliva z zapiski o njegovi biologiji

- Christian CAPAPÉ, Almamy DIABY, Youssof DIATTA, Sihem RAFRAFI-NOUIRA & Christian REYNAUD** Atypical Claspers in Smoothhound, *Mustelus mustelus* (Chondrichthyes: Triakidae) from the Coast of Senegal (Eastern Tropical Atlantic) 359
Netipična klasperja navadnega morskega psa, Mustelus mustelus (Chondrichthyes: Triakidae) iz senegalske obale (vzhodni tropski Atlantik)
- Hakan KABASAKAL, Ayşe ORUÇ, Ebrucan KALECIK, Efe SEVİM, Nilüfer ARAÇ & Cansu ILKILINÇ** Notes on a Newborn Kitefin Shark, *Dalatias licha*: New Evidence on the Nursery of a Rare Deep-Sea Shark in Northeastern Levant (Turkey) 367
Zapis o najdbi skotenega klinoplavutega morskega psa, Dalatias licha: novi dokaz o jaslicah redkega globokomorskega morskega psa v severovzhodnem levantu (Turčija)
- IHTIOLOGIJA
ITTILOGIA
ICHTHYOLOGY
- Nadia BOUZZAMMIT, Hammou EL HABOUZ, El hassen AIT-TALBORJT, Zahra OKBA & Hassan EL OUIZGANI** Diet Composition and Feeding Strategy of Atlantic Chub Mackerel *Scomber colias* in the Atlantic Coast of Morocco 377
Prehrana in prehranjevalna strategija lokarde (Scomber colias) ob atlantski obali Maroka
- FLORA
FLORA
FLORA
- Amelio PEZZETTA** Le Orchidaceae di Albona (Labin, Croazia) 393
Kukavičevke Labina (Hrvaška)
- FAVNA
FAVNA
FAVNA
- Murat BILECENOĞLU & Melih Ertan ÇINAR** The Mauve Stinger, *Pelagia noctiluca*, Has Expanded Its Range to the Sea of Marmara 405
Mesečinka (Pelagia noctiluca) je razširila svoj areal do Marmarskega morja
- Marijana HURE, Davor LUČIĆ, Barbara GANGAI ZOVKO & Ivona ONOFRI** Dynamics of Mesozooplankton Along the Eastern Coast of the South Adriatic Sea 411
Dinamika mezozooplanktona vzdolž vzhodne obale južnega Jadrana
- Abdelkarim DERBALI, Kandeel E. KANDEEL, Aymen HADJ TAIEB & Othman JARBOUI** Population Dynamics of the Cockle *Cerastoderma glaucum* (Mollusca: Bivalvia) in the Gulf of Gabes (Tunisia) 431
Populacijska dinamika navadne srčanke Cerastoderma glaucum (Mollusca: Bivalvia) v Gabeškem zalivu (Tunizija)
- Vasiliki K. SOKOU, Joan GONZALVO, Ioannis GIOVOS, Cristina BRITO & Dimitrios K. MOUTOPOULOS** Tracing Dolphin-Fishery Interaction in Early Greek Fisheries 443
Sledenje interakcij med delfini in ribiči v zgodnjih grških ribiških dejavnostih
- Pavel JAMNIK, Matija KRIŽNAR & Bruno BLAŽINA** Novi najdišči pleistocenske favne pod Kraškimi robom. Smo končno našli tudi jamo *Grotta dell'Orso*? 451
Two New Sites of Pleistocene Fauna under Karst Edge. Has a Grotta dell'Orso Cave Been Finally Found?
- OCENE IN POROČILA
RECENSIONI E RELAZIONI
REVIEWS AND REPORTS
- Andreja PALATINUS** Book Review: Plastic Pollution and Marine Conservation. Approaches to Protect Biodiversity and Marine Life 471
- Kazalo k slikam na ovitku 473
Index to images on the cover 473

DYNAMICS OF MESOZOOPLANKTON ALONG THE EASTERN COAST OF THE SOUTH ADRIATIC SEA

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ABSTRACT

Temporal and spatial variability of the mesozooplankton community was studied along the eastern coast of the south Adriatic Sea on a monthly basis from October 2012 to September 2013. Samples were collected at three stations using a 200 µm mesh Nansen net by vertical hauls at two depth layers. A total of 141 holoplanktonic taxa were identified, of which copepods were the dominant group. Total abundances showed high temporal variation (from 181 ind.m⁻³ in October to 1923 ind.m⁻³ in May). The mesozooplankton community differed significantly between the investigated layers and seasons. Deeper layers as well as the winter period were characterized by a subsurface and mesopelagic fauna, while over the warmer months the dominance of typically coastal Adriatic species was recorded. Comparing our results with studies carried out in the middle of the last century, it can be concluded that the eastern coast of the southern Adriatic hosts a stable mesozooplankton community, less affected by global changes.

Key words: copepods, seasonal variations, zooplankton, Mediterranean Sea

DINAMICA DEL MESOZOOPLANCTON LUNGO LA COSTA ORIENTALE DEL MARE ADRIATICO MERIDIONALE

SINTESI

La variabilità temporale e spaziale della comunità di mesozooplancton è stata studiata lungo la costa orientale dell'Adriatico meridionale su base mensile da ottobre 2012 a settembre 2013. I campioni sono stati raccolti in tre stazioni utilizzando una rete Nansen con maglie da 200 µm, con retate verticali a due strati di profondità. Sono stati identificati 141 taxa oloplanctonici, di cui i copepodi erano il gruppo dominante. Le abbondanze totali hanno mostrato un'elevata variazione temporale (da 181 ind.m⁻³ in ottobre a 1923 ind.m⁻³ in maggio). La comunità di mesozooplancton differiva significativamente tra gli strati e le stagioni analizzate. Gli strati più profondi e il periodo invernale sono stati caratterizzati da una fauna mesopelagica e sub-superficiale, mentre nei mesi più caldi si è registrata la dominanza di specie tipicamente costiere dell'Adriatico. Confrontando i nostri risultati con studi condotti a metà del secolo scorso, si può concludere che la costa orientale dell'Adriatico meridionale ospita una comunità di mesozooplancton stabile, meno influenzata dai cambiamenti globali.

Parole chiave: copepodi, variazioni stagionali, zooplancton, Mediterraneo

INTRODUCTION

The mesozooplankton occupy an essential position in pelagic carbon-flux processes since they serve as links between phytoplankton and higher pelagic trophic levels, such as larval and juvenile fishes, and interact with the benthic community. They are important indicators of climate change impact on marine and estuarine systems (Hays *et al.*, 2005; Hsiao *et al.*, 2011; Edwards *et al.*, 2013; Menéndez *et al.*, 2014; Varkitzi *et al.*, 2018). Data on spatial and temporal population variability and food-web interactions of zooplankton can be a valuable index of trophic dynamics and the ability of marine ecosystems to support marine fisheries.

The size range of the mesozooplankton (0.2-20 mm) corresponds almost exactly to the size range of copepodites and adult copepods, which are generally the dominant zooplankton group. Other members of the mesozooplankton include small hydromedusae, ctenophores, chaetognaths, appendicularians, doliolids, fish eggs and larvae, together with the older stages of crustacean plankton and meroplanktonic larvae. Different copepod species in various developmental stages may ingest a wide variety of prey and are mostly omnivorous, i.e., they are able to switch between suspension feeding on phytoplankton and ambush feeding on motile prey (Kiørboe, 1997) depending on the relative abundance of the different types of prey in the environment. Furthermore, small-sized copepods (<1 mm in length) are able to efficiently utilize components of the microbial food web (Turner, 2004). The occurrence of other taxa, such as cladocerans and gelatinous tunicates (appendicularians and doliolids) is more seasonal and characterized by high growth rates (Hopcroft & Roff, 1995; Rose, 2004).

Zooplankton respond rapidly to ecosystem disturbances and there is a strong correlation between environmental changes and plankton dynamics (Roemmich & McGowan, 1995). Temperature and salinity can directly influence growth rate and usually become dominant factors in determining the spatial and seasonal distribution of mesozooplankton (Badylak & Philips, 2008). Moreover, biotic interactions, including competition and predation, are also considered to control populations of mesozooplankton (Verity & Smetacek, 1996). In contrast to the offshore, the estuarine and coastal areas are systems with strong spatio-temporal variability in hydrobiological factors. Physical processes such as changes in water circulation patterns, variations in land inputs (sewage discharges, rivers, etc.) associated with coastline configurations, and bottom topography may also account for a significant part of the temporal variation in zooplankton community structure (Kurt & Polat, 2013). Therefore, studies of spatial and temporal variability of coastal zooplankton are important for

a better understanding of the functioning of coastal ecosystems, but also with respect to fisheries.

Seasonal variability of zooplankton has been studied in different coastal regions of the Mediterranean (Mazzocchi & Ribera d'Alcala, 1995; Siokou-Frangou, 1996; Siokou-Frangou *et al.*, 1998; Christou, 1998; Fernández de Puelles *et al.*, 2003, 2004, 2014; Jamet *et al.*, 2001, 2005; Zakaria, 2006; Mazzocchi *et al.*, 2011; Kurt & Polat, 2013; Vidjak *et al.*, 2019). Investigations of the zooplankton of the Adriatic coast have mostly focused on its productive northern part (Cataletto *et al.*, 1995; Fonda Umani *et al.*, 2005; Kamburska & Fonda Umani, 2006; Mackas *et al.*, 2012; Mozetič *et al.*, 2012; Bernardi Aubry *et al.*, 2012; Bojanić Varezić *et al.*, 2015; Pierson *et al.*, 2020). With regard to the eastern Adriatic coast, the copepod fauna of the Kvarner region was analyzed in the work of Hure *et al.* (1979), with several papers describing zooplankton communities in the coastal areas of the central Adriatic (Regner, 1985; Vidjak *et al.*, 2006, 2009, 2012). Zooplankton investigations of the southern shallow neritic areas have mostly focused on the more productive enclosed areas such as Mali Ston Bay (Benović & Onofri, 1982; Lučić & Kršinić, 1988; Lučić & Onofri, 1990;), Neretva Channel (Vidjak *et al.*, 2007, 2012), Mljet Lakes (Benović *et al.*, 2000; Miloslavić *et al.*, 2015) or inshore waters near Dubrovnik (Benović *et al.*, 1978). However, little information and data are available on species composition and seasonal variation of the zooplankton in the Dubrovnik offshore waters. Information on the current area mostly forms part of broader surveys of the open waters of the southern Adriatic. For example, Benović *et al.* (2004) presented data on medusae over the spring period in the central and southern Adriatic Sea. Additionally, a station near Dubrovnik has recently been involved in two investigations: studies of mesozooplankton over two transects in the southern Adriatic during winter, and presentation of copepod fauna in pre- and post-winter conditions in the southern Adriatic (Hure *et al.*, 2018, 2020, 2022).

However, this is the first comprehensive study of the zooplankton of the coastal waters surrounding Dubrovnik, including their taxonomic composition and annual pattern of abundance and diversity. The present study focuses on identifying the dominant environmental factors that drive species-specific spatial and temporal variability.

MATERIAL AND METHODS

Study area

The southern Adriatic is a relatively deep (up to 1250 m) oligotrophic circular basin. Interaction with the main body of the Mediterranean Sea includes inflow of Levantine Intermediate Water and Ionian

Surface Water northward along the eastern Adriatic coastline, and outflow southward along the western coast (Zore-Armanda, 1969; Orlić *et al.*, 1992; Gačić *et al.*, 2002). The intensity of the inflow varies depending on climatic oscillations and on the mechanism of the Bimodal Oscillating System that changes the circulation of the North Ionian Gyre from cyclonic to anticyclonic and vice versa, on a decadal time scale (Gačić *et al.*, 2010).

The study area, located near the city of Dubrovnik, is strongly influenced by currents originating from the eastern Mediterranean (Zore-Armanda, 1969; Gačić *et al.*, 2010). Furthermore, in such coastal areas, land runoff and inshore waters often interact with complex dynamics on a variety of temporal and spatial scales, and fluctuations in ecological parameters can be quite complex.

Sample collection and processing

Sampling was carried out during 11 monthly oceanographic surveys (from October 2012 to September 2013) at 3 stations: S1, S2 and S3. Instead

of the one sampling in March, two were conducted in April (at the beginning and end of the month). The stations were located along the eastern part of the southern Adriatic coast at a bottom depth of 100 m (Fig. 1). Due to difficult weather conditions, samples could not be collected at S3 in February 2013. Temperature, salinity and dissolved oxygen (DO) were measured using a SeaBird OC25 probe. Seawater samples (500 mL) for chlorophyll-a (Chl *a*) measurements were collected from depths of 0, 5, 10, 20, 50, 70 and 100 m using a Niskin bottle. For Chl *a*, seawater was filtered through Whatman GF/C glass-fiber filters. The filters were then homogenized in 90% aqueous acetone and the extract measured in a spectrophotometer according to the method described by Strickland & Parsons (1972).

A total of 64 mesozooplankton samples were collected from two depth layers (0-50 m, 50-100 m) using a vertically towed version of a modified open-closed Nansen net (1.13 m diameter; mesh size 200 μ m). Samples were collected in daylight and immediately preserved with buffered formaldehyde (4% final concentration). Sample processing and species identifica-



Fig 1: Study area with the sampling stations.

Sl. 1: Zemljevid obravnavanega območja z vzorčevalnimi postajami.

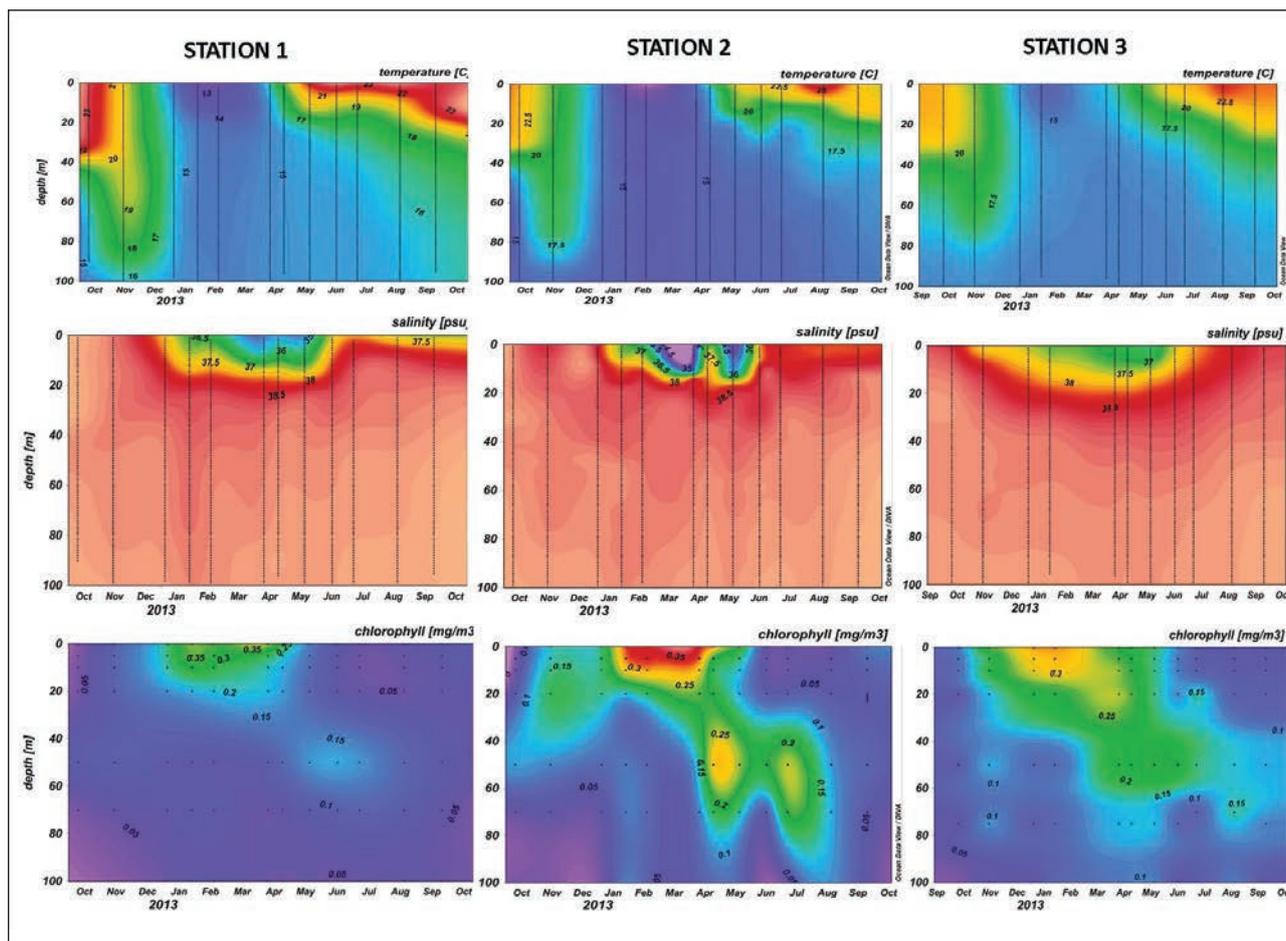


Fig. 2: Annual variability of temperature, salinity and Chl a in the South Adriatic.
Sl. 2: Letna variabilnost temperature, slanosti in Chl a v južnem Jadranu.

tion were conducted at the laboratory according to standard zooplankton methodology (Harris *et al.*, 2000), using an Olympus SZX16 stereomicroscope for counting and detailed observations. Each sample was examined in its entirety for rare species. Taxonomic identification was performed at the lowest possible taxonomical level: most of holoplankters were identified at the species level while some zooplankton were grouped in larger taxonomic groups (e.g., copepodite stages, copepod families Oncaeidae, Corycaeidae, Sapphirinidae, amphipods, ostracods, mysids, euphausiids, doliolids). Abundance was expressed as individuals per cubic meter (ind.m^{-3}).

Data analyses

For univariate biodiversity measures, the Margalef species richness (d) and Shannon-Wiener diversity index (H') were calculated for each sample to analyze seasonal diversity changes. The Margalef formula (Margalef, 1968) compares the number of

taxa in a sample and the total number of organisms comprising those taxa. The Margalef species richness index is given by the equation: $d = (S-1)/\ln N$, where S is the number of taxa in the sample and N is the total number of individuals. The Shannon-Wiener index (Shannon & Wiener, 1963) evaluates how individuals are distributed among taxa and is determined by the equation: $H' = -\sum_i P_i \ln P_i$, where P_i is the proportion that the i -th taxa represent to the total number of individuals in the sample space.

One-way analysis of similarity (ANOSIM) was used to test whether the community structure differed significantly between groups: investigated sites, layers and seasons (winter: J, F, spring: A, M, J, summer: J, A, S, Autumn: O, N). ANOSIM generated a test statistic, R , and the magnitude of R is the indicator of the degree of separation between groups, with the score of 1 indicating complete separation and 0 indicating no separation (Clarke & Green, 1988; Clarke, 1993).

Tab. 1: Average dissolved oxygen (DO) concentrations (ml/L) of each investigated layer at stations S1, S2 and S3. Tab. 1: Povprečna koncentracija raztopljenega kisika (DO) v ml/L na raziskanih slojih na postajah S1, S2 in S3.

Month	Layer	STATION		
		S1	S2	S3
OCT	0 - 50 m	4.97	5.03	5.03
	50 - 100 m	4.87	4.91	4.73
NOV	0 - 50 m	4.97	4.96	4.87
	50 - 100 m	5.05	5.15	4.70
JAN	0 - 50 m	5.21	5.17	5.21
	50 - 100 m	4.95	4.93	4.90
FEB	0 - 50 m	5.36	5.33	
	50 - 100 m	5.24	5.25	
APR	0 - 50 m	5.41	5.39	5.43
	50 - 100 m	5.20	5.21	4.90
APR	0 - 50 m	5.36	5.44	5.45
	50 - 100 m	5.12	5.14	5.21
MAY	0 - 50 m	5.38	5.48	5.49
	50 - 100 m	5.13	5.11	5.17
JUNE	0 - 50 m	5.26	5.25	5.21
	50 - 100 m	4.86	4.93	4.93
JULY	0 - 50 m	5.44	5.45	5.34
	50 - 100 m	4.85	4.99	5.02
AUG	0 - 50 m	5.66	5.58	5.36
	50 - 100 m	5.13	5.06	4.92
SEP	0 - 50 m	5.12	5.14	4.99
	50 - 100 m	4.95	4.82	4.84

The PRIMER 5 software package for Windows (Clarke & Gorley, 2001) was used to obtain diversity indices and conduct the ANOSIM analysis.

To identify taxa representative of the different layers and seasons, we employed Indicator Species Analysis (ISA; Dufrene & Legendre, 1997). This method combines information on the concentration of species abundance in a particular group and the consistency of occurrence of a species in a particular group. It generates an indicator value (IndVal) for each taxon, ranging from 0 (no indication) to 100 (perfect indication). The statistical significance of each taxa IndVal was determined by the Monte Carlo method, in which sample units were randomly reassigned 1000 times to test if the IndVal value was higher than expected by chance (Dufrene & Legendre, 1997). Taxa with IndVal > 25 and $p < 0.1$ were considered characteristic of the groups.

Non-metric multidimensional scaling (NMDS) ordination was used to detect relationships between major zooplankton taxa (>3% contribution) and environmental variables (temperature, salinity, Chl *a* and DO). Prior to the analyses, the data were log-transformed to normalize the variance while maintaining the distances between low values. The

final matrix consisted of 64 samples and 19 taxa. The Bray-Curtis measure was used. Dimensionality was determined through evaluation of the standard residual sum of squares (STRESS; Mather, 1976). STRESS values of less than 20 indicate a stable solution (McCune & Grace, 2002). The ISA and NMDS analyses were performed using PC-ORD v. 5.32 (McCune & Mefford, 2006).

RESULTS

Environmental conditions

The annual variations in temperature, salinity and Chl *a* are shown in Fig. 2. The greatest temperature fluctuations were recorded at the surface, particularly at S2, where a minimum of 12.6 °C (February) and a maximum of 25.7 °C (August) were recorded. A period of isothermal conditions occurred from December to April at all stations. Sea surface temperature increased from the end of April, with the strongest thermal stratification in August between 10 and 20 m depth.

The vertical salinity distribution shows that the largest fluctuations occurred in the upper 20 m, due to lateral advection of fresh water from the coast. This was most evident at station S2, where a sharp halocline was detected in spring (minimum of 34.6 recorded at the surface in April). Layers below 20 m are characterized by high salinity values (>38.5) with a maximum of 39.0 noticed at the S3, in October at 30 m depth.

During the study period, the water column was well oxygenated (Tab. 1), with DO concentrations ranging from 4.4 ml/L (S3; October; bottom layers) to 5.9 ml/L (S1; August; 25 m depth).

The highest variations in Chl *a* concentration were recorded at S1, from a minimum of 0.01 mg.m⁻³, recorded in the bottom layer in October 2012 to 0.64 mg.m⁻³ found at the surface in April. Generally, the highest values were recorded in the surface layers of S2 during spring, with a maximum of 0.36 mg.m⁻³.

Mesozooplankton abundance and distribution

Zooplankton abundances in the surface layers (0-50 m) ranged between 346 ind.m⁻³ in October (S1) and 2357 ind.m⁻³ in August (S1) with an average value of 983±553 ind.m⁻³ (Figs. 3 a, b, c). The bottom layers (50-100 m) generally had lower zooplankton abundance than the upper, with an average density of 517±329 ind.m⁻³. The minimum (181 ind.m⁻³) was also found in October at S1 (Fig. 3d), and the maximum (1013 ind.m⁻³) was recorded in April at S3 (Fig. 3f). The increased abundances were generally recorded in spring, following the trend of the copepods as the dominant group com-

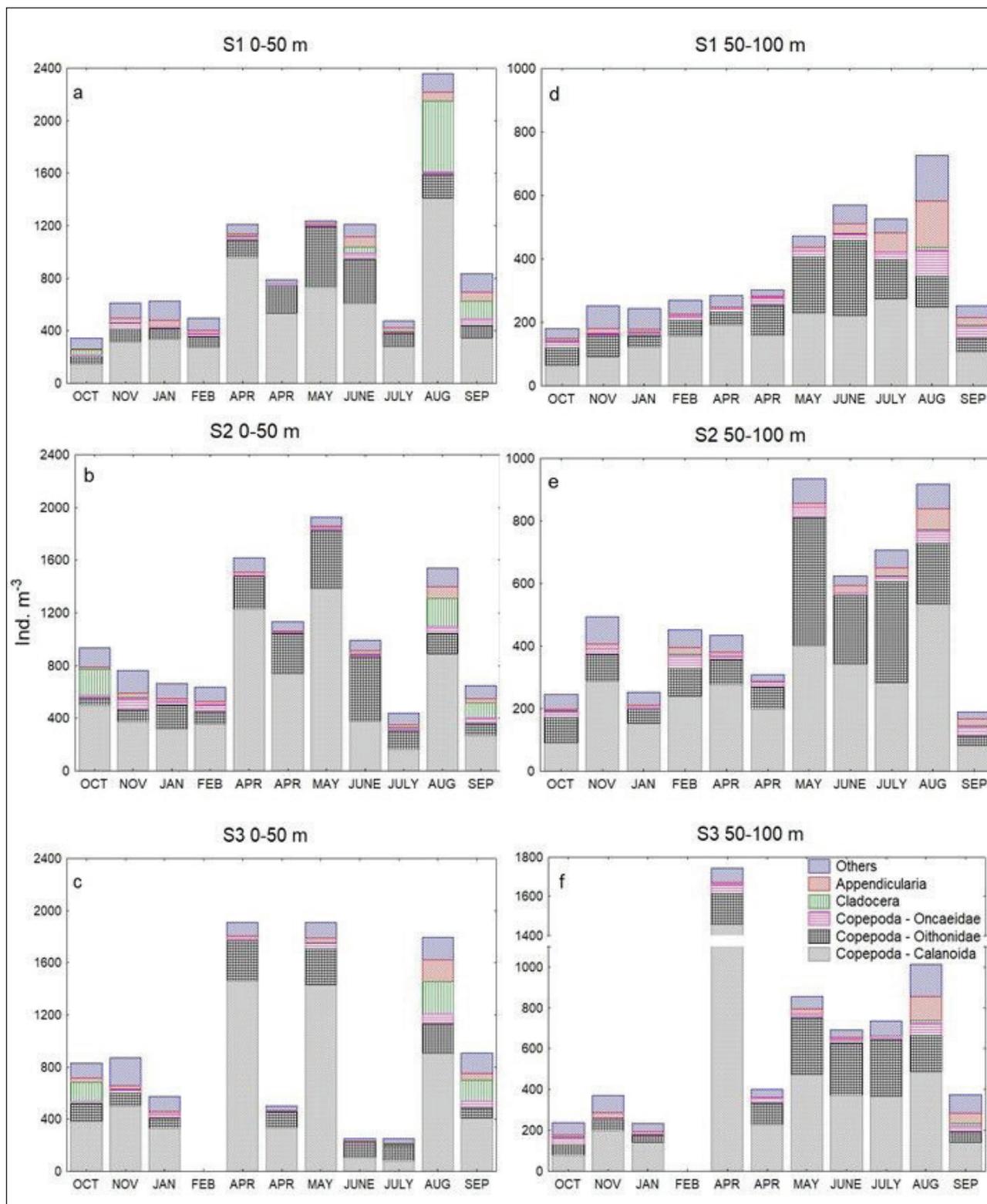


Fig. 3: Annual distribution of the abundances of all mesozooplankton and the dominant mesozooplankton groups at stations S1, S2 and S3 in the upper layer (a, b, c) and in the bottom layer (d, e, f).
Sl. 3: Letna porazdelitev abundance celotnega mezozooplanktona in prevladujočih mezozooplanktonskih skupin, na postajah S1, S2 in S3 v zgornjem sloju (a, b, c) in v spodnjem sloju (d, e, f).

prising from 60 to 98% (mean: 82%) of the total. On average, copepods were more numerous in the upper layer ($796 \pm 490 \text{ ind.m}^{-3}$) than in the lower ($427 \pm 310 \text{ ind.m}^{-3}$). Calanoids were the dominant group and their copepodites were more abundant than adults, representing on average 67% of the total of calanoids at all stations. Oithonidae were more numerous only in spring in the layer below 50 m (stations S1 and S2). Oncaeididae were more abundant in the bottom layer during the summer, especially at S1.

Appendicularians were the second most important mesozooplankton group with the highest abundances in August (up to 145 ind.m^{-3}), especially in the layers below 50 m depth. Cladocerans were found mainly in the surface layers and were relatively important from August to October, contributing 17% on average. Of the other invertebrates, doliolods were relatively more abundant, especially in the bottom layer, where they reached a maximum average abundance of 112 ind.m^{-3} in August. Chaethognats were more abundant in the upper layer ($16 \pm 10 \text{ ind.m}^{-3}$) than in the layer below ($6 \pm 5 \text{ ind.m}^{-3}$). Meroplanktonic groups fluctuated significantly in time and space (total average of $36 \pm 10 \text{ ind.m}^{-3}$) with bivalvia larvae being the most abundant taxon.

Mesozooplankton diversity and community structure

A total of 141 holoplanktonic taxa were identified (Appendix 1). Copepods were the most important group in terms of diversity with 71 taxa found, followed by hydromedusae (18), appendicularians (14) and siphonophores (13). The annual trend of diversity showed a clear seasonal pattern, with the lowest values registered in spring and increasing over winter (Fig. 4). Generally, higher diversity was found in the 50–100 m layer (average $d=9.0$; $H'=2.9$) than in the upper 50 m ($d=8.4$; $H'=2.8$).

The most abundant and regular adult copepods were calanoids and cyclopoids, including *Oithona similis* (average contribution 8.2%), *Ctenocalanus vanus* (4.2%), *Acartia (Acartiura) clausi* (4.1%), Oncaeididae (3.4%) and *Oithona nana* (3.0%). Harpacticoid density was low, mainly due to the variability of the most important species of the group – *Euterpina acutifrons* (average contribution 0.3%). Apart from copepods, a larger contribution to the entire community was noted for Cladocera *Penilia avirostris* (3.4%), the doliolids (1.4%) and Appendicularia *Oikopleura longicauda* (1.1%).

ANOSIM analyses showed no statistically significant difference between sampling stations (ANOSIM global $R=-0.026$, $P>0.01$), while significant differences were observed between sampling

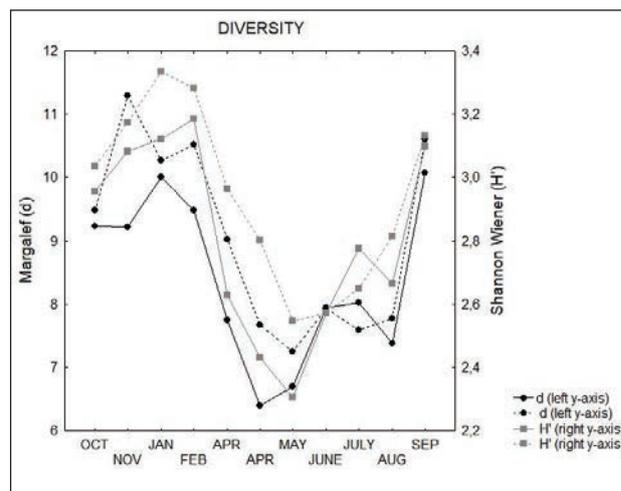


Fig. 4: Annual diversity distribution in the upper layer (full line) and in the bottom layer (dotted line). H' = Shannon's diversity index, D = Margalef's species richness index.

Sl. 4: Letna porazdelitev diverzitet v zgornjem (neprekinjena črta) in globinskem sloju (prekinjena črta). H' = Shannonov diverzitetni indeks, D = Margalefov indeks vrstne pestrosti.

layers (global $R=0.265$, $P<0.01$) and seasons (global $R=0.591$, $P<0.01$). When considering seasons, significant differences were noted between spring/autumn samples ($R=0.738$), attributable to different zooplankton composition, while the least differences were observed between summer and autumn samples ($R=0.368$).

Indicative taxa ($\text{IndVal}>25$; $p<0.1$), with their abundances and the contribution of each layer and season are shown in Table 2. Most of the mesozooplankton that characterized the upper layer were coastal or warm water taxa (e.g., Corycaeidae). By contrast, the deeper layers were occupied by subsurface and mesopelagic copepods (e.g., *Lucicutia flavicornis*, *Haloptilus longicornis*, genus *Pleuromamma*). In winter, the most important taxa were also copepod species that are generally found in open waters (e.g., *L. clausi*, *P. abdominalis*). In spring, cyclopoids of the genus *Oithona* showed the highest abundances while *Paracalanus parvus* showed the highest IndVal . The pteropod *Limacina trochiformis*, doliolids, the appendicularian species *Fritillaria pellucida* and *Oikopleura fusiformis*, the cladoceran *P. avirostris* and the calanoid genus *Centropages* (*C. typicus* and *C. kroyeri*) characterized the summer period along the southeastern Adriatic coast. In autumn, only five mesozooplankton taxa displayed $\text{IndVal}>25$ and were composed of highly heterogenic members, including copepod genus *Calocalanus*, dinoflagellate *Noctiluca scintillans*, ostracods, and hydromedusae *Liriope tetraphylla*.

Tab. 2: Mesozooplankton taxa characterizing each depth layer and seasons with their indicator values (IndVal), average abundance (N - ind. m⁻³) and average contribution (%).**Tab. 2: Mezozooplanktonski taksoni, značilni za oba sloja in sezone z njihovimi indikatorskimi vrednostmi (IndVal), povprečno abundanco (N - os.m⁻³) in povprečnim deležem (%).**

	IndVal	N	%		IndVal	N	%
Upper layer (0-50 m)				Bottom layer (50-100 m)			
<i>Corycaeidae</i>	77.9	18.3	2.2	<i>Tomopteris</i> spp.	67.1	0.6	0.1
<i>Temora stylifera</i>	77.4	7.4	0.8	<i>Lucicutia flavicornis</i>	63.8	1.8	0.6
<i>Flaccisagitta enflata</i>	71.8	1.8	0.2	<i>Diaixis pygmaea</i>	61.4	1.7	0.3
<i>Acartia (Acartiura) clausi</i>	68.8	58.1	4.2	<i>Clausocalanus paululus</i>	60.3	5.0	1.4
<i>Muggiaea kochii</i>	63.5	1.4	0.2	<i>Haloptilus longicornis</i>	46.8	2.9	1.0
<i>Aglaura hemistoma</i>	62.9	1.4	0.2	<i>Pleuromamma gracilis</i>	43.0	0.5	0.2
<i>Creseis</i> spp.	62.2	5.1	0.7	<i>Pleuromamma abdominalis</i>	37.5	0.2	0.1
<i>Euterpina accutifrons</i>	61.5	3.4	0.4	<i>Scolecithricella dentata</i>	36.8	0.3	0.1
<i>Evadne spinifera</i>	57.5	7.0	0.7				
<i>Isias clavipes</i>	44.1	1.7	0.1				
<i>Pseudevadne tergestina</i>	28.1	2.8	0.2				
Winter				Spring			
<i>Euterpina accutifrons</i>	63.1	6.3	1.2	<i>Paracalanus parvus</i>	58.0	14.6	1.4
<i>Haloptilus longicornis</i>	55.9	4.3	1.7	Hyperiididae	57.1	3.5	0.6
<i>Lucicutia clausi</i>	52.6	2.3	0.7	<i>Ctenocalanus vanus</i>	55.8	55.4	5.6
<i>Pleuromamma abdominalis</i>	44.9	0.6	0.3	<i>Acartia (Acartiura) clausi</i>	55.3	56.4	4.3
<i>Lucicutia flavicornis</i>	46.0	2.3	0.9	<i>Oithona similis</i>	54.8	108.8	12.9
<i>Euchaeta marina</i>	37.9	0.4	0.1	<i>Calanus helgolandicus</i>	54.6	3.9	0.5
<i>Neocalanus gracilis</i>	39.6	0.4	0.1	<i>Oithona nana</i>	53.4	39.7	4.4
				<i>Serratosagitta serratodentata</i>	31.4	0.1	<0.1
Summer				Autumn			
<i>Limacina trochiformis</i>	66.6	4.7	0.8	Ostracoda	58.6	14.4	3.7
<i>Doliolida</i>	64.4	25.4	2.8	<i>Calocalanus styliremis</i>	52.0	8.5	1.5
<i>Fritillaria pellucida</i>	59.2	14.8	2.1	<i>Calocalanus elongatus</i>	50.0	0.5	0.1
<i>Centropages typicus</i>	58.0	14.7	1.3	<i>Noctiluca scintillans</i>	49.1	18.2	3.6
<i>Oikopleura (Coecaria) fusiformis</i>	55.9	11.2	1.5	<i>Liriope tetraphylla</i>	41.7	0.1	<0.1
<i>Penilia avirostris</i>	53.8	61.5	4.6				
<i>Lizzia blondina</i>	38.9	0.2	<0.1				
<i>Centropages kroyeri</i>	32.5	1.9	0.1				

The ordination of the major taxa, with the highest IndVal and an overall contribution of >3% related to environmental factors, is shown in Fig 5. A 2D NMDS ordination solution was chosen based on the final moderate stress value of 15.6 and the final instability <0.000001. The ordination cumulatively represented 80.6% of the community variance. Axis 1 represented 38.8% of the variance and was related to temperature variation ($r=0.737$). Thus, this axis distinguished summer from winter samples. The cladoceran *Penilia*

avirostris was strongly associated with summer high-temperature samples, while the copepod *Clausocalanus paululus* displayed the opposite pattern. Axis 2 explained 41.8% of the remaining variance and was positively correlated with DO ($r=0.462$) and negatively with salinity ($r=-0.436$). Distribution of samples (grouped by season) along the second axes confirmed the strong separation between spring and winter/autumn samples where the spring samples were grouped with higher DO values.

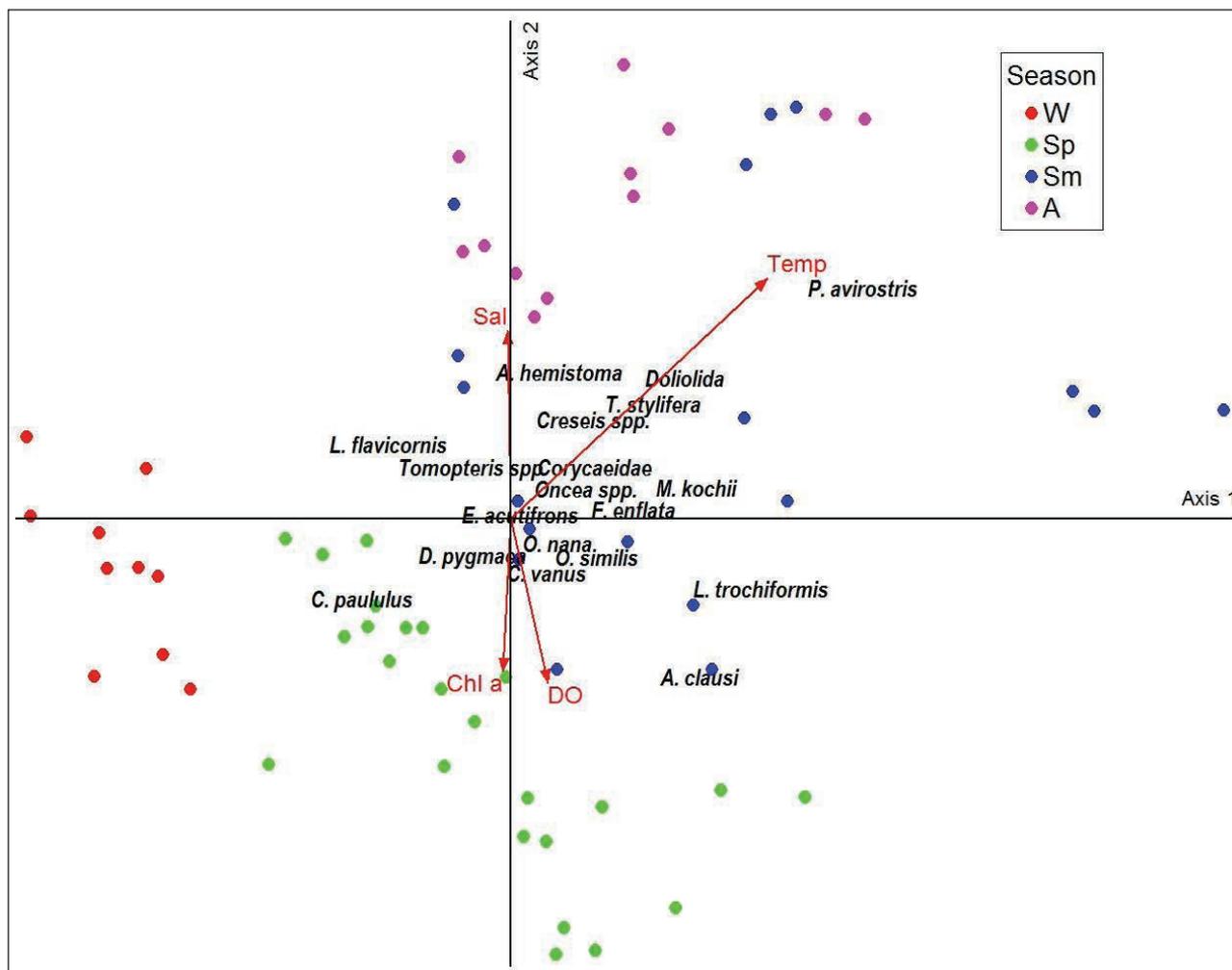


Fig. 5: Ordination joint plot with results of nonmetric multidimensional scaling (NMDS) with the position of the most important taxa and the related environmental variables overlaid as vectors (Temp-temperature, Sal – salinity, Chl a, DO). Vector length and direction indicate relative strength of the correlation with axes. Samples were grouped by season (W - winter, Sp - spring, Sm - summer, A - autumn).

Sl. 5: Ordinacijski diagram z rezultati nemetričnega večdimenzionalnega skaliranja (NMDS) s položajem najpomembnejših taksonov in povezanimi okoljskimi spremenljivkami kot vektorji (Temp - temperatura, Sal - slanost, Chl a, DO). Dolžina in smer vektorja označujeta relativno moč korelacije z osmi. Vzorci so bili razvrščeni po sezonah (W - zima, Sp - pomlad, Sm - poletje, A - jesen).

DISCUSSION

In this study, the annual distribution of mesozooplankton in the coastal area of the Dubrovnik region was investigated with the aim of providing detailed information on their composition, biodiversity and relationship with environmental parameters.

Total mesozooplankton values were considerably lower compared to other coastal Mediterranean regions (Siokou-Frangou, 1996; Fernández de Puellas *et al.*, 2003; Ribera d'Alcala *et al.*, 2004; Kurt & Polat, 2013) or other eastern Adriatic coastal sites (Hure *et al.*, 1979; Vidjak *et al.*, 2007, 2012; Miloslavić *et al.*, 2015).

Similar abundance ranges were found in the open surface waters of southern Adriatic (Hure *et al.*, 2018), indicating low productivity, negligible human impact and a high influence of the open sea. Despite the proximity of the mouth of a stream whose freshwater discharge causes lower surface salinities in spring (affecting station S2 the most) Chl a values also remain low, analogous to those found in offshore waters (Benović *et al.*, 2004; Hure *et al.*, 2018, 2020), confirming the oligotrophic nature of the study sites.

In Mediterranean coastal areas, zooplankton abundance generally follows the phytoplankton bloom that takes place in late winter, with increased

values in spring/summer (Siokou-Frangou, 1996; Ribera d'Alcala *et al.*, 2004; Morabito *et al.*, 2018) and/or bimodal distribution with a second peak in autumn (Scotto di Carlo & Ianora, 1983; Morabito *et al.*, 2018). Generally, our results show higher values during spring and summer. Unlike more eutrophic coastal Mediterranean sites, where cladocerans (mostly *Penilia avirostris*) dominate during the summer (Siokou-Frangou, 1996; Calbet *et al.*, 2001; Vidjak *et al.*, 2007; Isari *et al.*, 2007; Camatti *et al.*, 2008; Piontkovski *et al.*, 2012; Bernardi Aubry *et al.*, 2012; Peirson *et al.*, 2020) and have a great influence on total mesozooplankton densities, our total abundances in the surface layers followed copepod densities even during the August/September. Thus, the lack of seasonal predominance of cladocerans indicates a negligible coastal influence in the study area. In the bottom layers, the summer peak was associated with the higher densities of doliolids and appendicularians, which were found to be the most important group after copepods. Their temperature-dependent seasonality has been frequently documented (Lučić & Onofri, 1990; Vidjak *et al.*, 2007; Isari *et al.*, 2007; Miloslavić *et al.*, 2015). Compared to other more productive surrounding areas where cyclopoids (Oithonidae) prevail over copepod fauna during summer (Lučić & Kršinić, 1998; Vidjak *et al.*, 2007; Miloslavić *et al.*, 2015), calanoids remained dominant in our study for almost the entire period of investigation.

All the species identified during this research have already been recorded in the Adriatic Sea (Hure *et al.*, 1980; Benović *et al.*, 2004; Batistić *et al.*, 2004; Hure *et al.*, 2018). The most abundant copepod taxa, such as *Oithona similis*, *Ctenocalanus vanus*, *Acartia (Acartiura) clausi*, *Oithona nana* and Oncaeidae, are similar to those reported for other coastal Adriatic areas (Hure *et al.*, 1979; Hure & Kršinić, 1998; Vidjak *et al.*, 2012; Miloslavić *et al.*, 2015), confirming a relative uniformity of the copepod community in coastal Adriatic waters. Even so, their numbers over the investigated sampling sites were considerably lower than in other coastal areas.

The studied area is characterized by a high influence of open-water intrusion, including inflowing Ionian currents (Gačić *et al.*, 2002), which have a great impact on the distribution of zooplankton species (Hure *et al.*, 2018). It should be emphasized here that some taxonomic groups, whose members show high species-specific differences, were not determined at species level but at family level (e.g., Corycaeidae, Oncaeidae, Ostracoda). Although station S2 was under a greater influence of low salinity water inflow, i.e., terrestrial runoff, than the other two investigated stations, this influence seems to have a negligible effect on the mesozooplankton community, which did not differ between stations.

Moderate differences were found in the vertical levels, where neritic species occupied the surface layer, while mainly subsurface (*Tomopteris* spp., *Clausocalanus paululus*, *Lucicutia flavicornis*, *Pleuromamma gracilis*) and mesopelagic (*Pleuromamma abdominalis*, *Haloptilus longicornis*, *Scolecithricella dentata*) taxa were indicative of the bottom layer.

In general, seasonality was a major factor influencing the distribution of zooplankton in the study area. The NMDS analysis revealed that seasonal temperature changes were the main environmental gradient responsible for the formation of the first axis. It is well known that temperature is an important factor regulating the distribution of zooplankton (Siokou-Frangou *et al.*, 2004; Vidjak *et al.*, 2007, 2012; Miloslavić *et al.*, 2015). There is a strong separation of winter samples from all others along this axis, with mid-temperature (*C. paululus*) and termophilic (*P. avirostris*, *T. stylifera*, Doliolids) taxa also being distinguished. The winter period along the southern Adriatic coast was characterized by low densities and presence of characteristic offshore species, with the exception of *E. acutifrons* at the surface. *E. acutifrons* also peaked in winter in the Neretva Channel (Vidjak *et al.*, 2007), and in even greater numbers. The spread of subsurface and intermediate copepod species from southern and central Adriatic along the eastern coast winter isotherm has already been reported (Regner, 1985; Hure & Kršinić, 1998; Vidjak *et al.*, 2007). This is related to the eastern Adriatic circulation pattern, which is characterized by an increased inflow enhancing currents along the eastern coast (Zore-Armanda *et al.*, 1999; Boicourt *et al.*, 2020). The annual diversity pattern over the study period also confirmed this condition.

The most significant differences in the zooplankton community were found between spring and autumn samples, as displayed by the results of the NMDS analysis along the second axis. The environmental traits characterizing the spring samples, on the other hand, are low salinity and higher Chl *a* and DO values. Typical coastal copepods (*Paracalanus parvus*, *Acartia (Acartiura) clausi*) were conspicuous, as were species of the genus *Oithona*, whose dominance over the warmer part of the year has already been reported in the eastern Adriatic coast (Vidjak *et al.*, 2007; Miloslavić *et al.*, 2015).

Autumn was distinguished by cold water taxa, such as the copepod genus *Calocalanus* and ostracods, which are an important element of the southern Adriatic winter zooplankton community (Hure & Kršinić, 1998; Brautović *et al.*, 2006). Dinoflagellates of the species *Noctiluca scintillans* also showed higher abundances in this part of the year, although their blooms normally occur in the spring-summer period (Fonda Umani, 2004; Mikaelyan *et al.*, 2014).

During summer, in addition to the copepod genus *Centropages*, other zooplankton groups and taxa were conspicuous, including the pteropod *Limacina trochiformis* or appendicularians *Fritillaria pellucida* and *Oikopleura fusiformis*. These species usually peak in spring or summer (Siokou-Frangou, 1996; Calbet, 2001; Ribera d'Alcala *et al.*, 2004; Miloslavić *et al.*, 2015).

CONCLUSIONS

It can be concluded that the mesozooplankton fauna of the investigated area is marked by high dynamics and a high degree of temporal variability due to the particular hydrographic regime and occurrence of characteristic taxa in the annual cycle. The low values of Chl *a* and total abundance of mesozooplankton pointed to the oligotrophic character of the studied area, indicating a negligible influence of the nearby freshwater source or the Boka Kotorska system located further south. In the warmer months, higher neritic zooplankton abundances were recorded in the upper layers. In winter, strong and persistent physical forces maintain the homogeneity of the water column and therewith higher salinity, promoting the presence of species characteristic of the open sea, greater diversity, and decrease in overall densities. There are several studies confirming significant changes in the composition and abundance of mesozooplankton in the Adriatic Sea as a result of global warming and introduction of non-native species, especially in its northern region (Conversi *et al.*, 2009; Bernardi Aubry *et al.*, 2012; Mozetič *et al.*, 2012; Pierson *et al.*, 2020). Overall, the authors found that the species preferring cold water decreased while species with a preference for warm water expanded

their residence and migrated northwards. This was mostly related to summer–autumn increases in sea surface temperature.

This investigation could be of particular importance as a database for future monitoring of the planktonic communities of the Adriatic Sea, representing a baseline study of the zooplankton biodiversity of the eastern Adriatic coastal system, fundamental for future considerations about the possible measures to mitigate to the effects of climate change and anthropogenic activities.

However, a major limitation in describing the annual cycles is the remarkable complexity and interannual variability of environmental factors and plankton responses. This is particularly evident in oligotrophic waters, where short-term and/or small-scale patchiness may be of greater importance. More frequent sampling and multi-year surveys are therefore needed to cover all phases of an annual cycle and to distinguish regular patterns from occasional and exceptional events in this variable system.

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Appendix 1: List of determined zooplankton taxa found in the eastern coast of the south Adriatic in 2012/2013. An Asterisk indicates presence in investigated layer and season (W-winter, Sp-spring, Sm-summer, A-Autumn). Priloga 1: Seznam določenih taksonov zooplanktona, najdenih na vzhodni obali južnega Jadrana v letih 2012/2013. Zvezdica označuje prisotnost v preiskovanem sloju in sezoni (W-zima, Sp-pomlad, Sm-poletje, A-jesen).

Taxon	Layer		Season			
	0-50 m	50-100 m	W	Sp	Sm	A
HOLOPLANKTON						
Cnidaria Hydrozoa						
Order Anthoathecata						
<i>Podocorynoides minima</i>	*	*	*		*	
<i>Lizzia blondina</i>	*	*			*	
<i>Podocoryna areolata</i>		*			*	
<i>Odessia maeotica</i>	*				*	
<i>Euphysa aurata</i>		*		*	*	
<i>Turritopsis dohrnii</i>	*					*
<i>Eucodonium brownei</i>	*					*
Order Leptothecata						
<i>Obelia</i> spp.	*	*	*	*	*	
<i>Clytia hemisphaerica</i>	*	*	*	*	*	*
<i>Helgicirra cari</i>	*	*			*	
<i>Eutima gracilis</i>	*				*	
Order Trachymedusae						
<i>Rhopalonema velatum</i>	*	*	*	*	*	*
<i>Aglaura hemistoma</i>	*	*	*	*	*	*
<i>Persa incolorata</i>	*	*	*	*	*	*
Order Limnomedusae						
<i>Liriope tetraphylla</i>	*	*			*	*
Order Narcomedusae						
<i>Solmissus albescens</i>		*			*	*
<i>Solmaris leucostyla</i>		*			*	*
<i>Solmundella bitentaculata</i>	*	*	*		*	
Order Siphonophorae (Calycophorae)						
<i>Sulculeolaria chuni</i>	*				*	
<i>Sulculeolaria quadrivalvis</i>	*		*			
<i>Lensia campanella</i>	*	*	*			*
<i>Lensia fowleri</i>		*		*		
<i>Lensia multicristata</i>		*	*			
<i>Lensia subtilis</i>	*	*	*	*	*	*
<i>Muggiaea atlantica</i>	*	*	*	*	*	*
<i>Muggiaea kochii</i>	*	*	*	*	*	*
<i>Chelophyes appendiculata</i>	*	*			*	
<i>Eudoxoides spiralis</i>	*	*	*	*	*	*
<i>Sphaeronectes irregularis</i>		*			*	
<i>Sphaeronectes koellikeri</i>	*	*	*	*	*	*

<i>Bassia bassensis</i>	*	*	*		*	*
Ctenophora	*	*			*	*
Mollusca Gastropoda						
Order Littorinimorpha						
<i>Atlanta peronii</i>	*	*	*		*	*
Order Thecosomata						
<i>Limacina</i> sp.	*					*
<i>Limacina trochiformis</i>	*	*	*	*	*	*
<i>Heliconoides inflatus</i>	*	*	*	*	*	*
<i>Creseis</i> spp.	*	*	*	*	*	*
Annelida (Polychaeta)						
<i>Tomopteris</i> spp.	*	*	*	*	*	*
Chaetognatha Sagittoidea						
<i>Flaccisagitta enflata</i>	*	*	*	*	*	
<i>Mesosagitta minima</i>	*	*		*		*
<i>Parasagitta setosa</i>	*	*	*	*	*	*
<i>Serratasagitta serratodentata</i>	*	*		*	*	
<i>Decipisagitta descipiens</i>	*	*	*	*		
Arthropoda Crustacea						
Superorder Cladocera						
<i>Penilia avirostris</i>	*	*		*	*	*
<i>Evadne spinifera</i>	*	*	*	*	*	*
<i>Evadne nordmanni</i>	*			*	*	*
<i>Pseudevadne tergestina</i>	*				*	*
<i>Pleopis polyphemoides</i>	*	*	*	*	*	*
<i>Podon intermedius</i>	*			*	*	
Class Ostracoda	*	*	*	*	*	*
Subclass Copepoda						
<i>Calanus helgolandicus</i>	*	*	*	*	*	*
<i>Mesocalanus tenuicornis</i>	*	*	*	*	*	*
<i>Nannocalanus minor</i>	*	*	*	*	*	*
<i>Neocalanus gracilis</i>	*	*	*	*	*	*
<i>Pareucalanus attenuatus</i>	*	*	*	*	*	*
<i>Paracalanus parvus</i>	*	*	*	*	*	*
<i>Paracalanus denudatus</i>	*	*	*	*	*	*
<i>Calocalanus pavo</i>	*	*	*	*	*	*
<i>Calocalanus contractus</i>	*	*	*	*	*	*
<i>Calocalanus styliremis</i>	*	*	*	*	*	*
<i>Calocalanus elongatus</i>	*	*	*		*	*
<i>Mecynocera clausi</i>	*	*	*	*	*	*
<i>Clausocalanus arcuicornis</i>	*	*	*	*	*	*
<i>Clausocalanus jobei</i>	*	*	*	*	*	*
<i>Clausocalanus furcatus</i>	*	*	*	*	*	*
<i>Clausocalanus pergens</i>	*	*	*	*	*	*
<i>Clausocalanus parapergens</i>	*	*		*	*	*

<i>Clausocalanus lividus</i>	*	*	*	*	*	*
<i>Clausocalanus mastigophorus</i>	*	*	*	*	*	*
<i>Clausocalanus paululus</i>	*	*	*	*	*	*
<i>Ctenocalanus vanus</i>	*	*	*	*	*	*
<i>Pseudocalanus elongatus</i>	*	*		*	*	*
<i>Aetideus armatus</i>	*	*	*	*	*	*
<i>Aetideus giesbrechti</i>	*	*	*	*		
<i>Paraeuchaeta hebes</i>	*	*	*	*	*	*
<i>Euchaeta marina</i>	*	*	*	*		*
<i>Xanthocalanus agilis</i>		*	*	*		
<i>Spinocalanus longicornis</i>		*				*
<i>Scaphocalanus curtus</i>	*	*	*	*	*	*
<i>Scolecithricella dentata</i>	*	*	*	*	*	*
<i>Scolecithrix bradyi</i>	*	*	*	*	*	*
<i>Diaixis pygmaea</i>	*	*	*	*	*	*
<i>Centropages typicus</i>	*	*	*	*	*	*
<i>Centropages kroyeri</i>	*			*	*	*
<i>Centropages violaceus</i>	*					*
<i>Isias clavipes</i>	*	*	*	*	*	*
<i>Temora stylifera</i>	*	*	*	*	*	*
<i>Temora longicornis</i>	*				*	
<i>Pleuromamma abdominalis</i>		*	*	*	*	*
<i>Pleuromamma gracilis</i>	*	*	*	*	*	*
<i>Labidocera wollostoni</i>		*		*		
<i>Lucicutia flavicornis</i>	*	*	*	*	*	*
<i>Lucicutia ovalis</i>	*	*	*	*	*	*
<i>Lucicutia clausi</i>	*	*	*	*	*	
<i>Lucicutia gemina</i>		*		*		
<i>Heterorhabdus papilliger</i>	*	*	*	*		*
<i>Heterorhabdus abyssalis</i>		*		*		
<i>Heterorhabdus spinifrons</i>		*	*			
<i>Haloptilus longicornis</i>	*	*	*	*	*	*
<i>Candacia giesbrechti</i>	*	*	*	*	*	*
<i>Candacia bipinata</i>		*	*			
<i>Phaenna spinifera</i>	*	*	*			*
<i>Acartia (Acartiura) clausi</i>	*	*	*	*	*	*
<i>Acartia (Acartiura) longiremis</i>	*	*	*		*	*
<i>Acartia (Acartia) negligens</i>	*		*			
<i>Oithona nana</i>	*	*	*	*	*	*
<i>Oithona plumifera</i>	*	*	*	*	*	*
<i>Oithona similis</i>	*	*	*	*	*	*
<i>Oithona setigera</i>	*	*	*	*	*	*
<i>Oithona atlantica</i>	*	*		*	*	
<i>Oithona linearis</i>	*	*			*	*
<i>Oncea spp.</i>	*	*	*	*	*	*

<i>Euterpina acutifrons</i>	*	*	*	*	*	*
<i>Microsetella norvegica</i>	*	*	*		*	*
<i>Macrosetella gracilis</i>	*	*	*	*	*	*
Corycaeidae	*	*	*	*	*	*
<i>Goniopsillus clausi</i>	*	*	*	*	*	*
<i>Lubbockia squillimana</i>	*	*	*	*	*	*
<i>Copilia</i> spp.	*	*	*			
<i>Sapphirina</i> spp.	*	*	*	*	*	*
<i>Monstrilla longiremis</i>	*			*	*	
Order Euphausiacea	*	*	*	*	*	*
Order Mysida	*	*		*	*	
Order Isopoda	*	*			*	*
Order Amphipoda Hyperiidea	*	*	*	*	*	*
Chordata Thaliaceae						
Order Doliolida	*	*	*	*	*	*
Chordata Appendicularia						
<i>Oikopleura (Vexillaria) albicans</i>	*		*			
<i>Oikopleura (Vexillaria) dioica</i>	*	*	*	*	*	*
<i>Oikopleura (Coecaria) longicauda</i>	*	*	*	*	*	*
<i>Oikopleura cophocerca</i>		*	*	*		
<i>Oikopleura (Coecaria) fusiformis</i>	*	*	*	*	*	*
<i>Appendicularia sicula</i>	*	*			*	
<i>Mesoikopleura haranti</i>		*			*	
<i>Fritillaria borealis</i>	*	*	*	*	*	*
<i>Fritillaria pellucida</i>	*	*	*	*	*	*
<i>Fritillaria haplostoma</i>	*	*	*	*	*	*
<i>Fritillaria formica</i>	*	*		*	*	
<i>Fritillaria megachile</i>	*		*			
<i>Stegosoma magnum</i>		*				*
<i>Kowalevskia tenuis</i>	*				*	
MEROPLANKTON						
Decapoda	*	*	*	*	*	*
Bivalvia	*	*	*	*	*	*
Phoronida	*	*	*	*	*	*
Gastropoda	*	*	*	*	*	*
Polychaeta	*	*	*	*	*	*
Cirripedia	*	*		*	*	
Echinodermata Bipinnaria	*	*	*	*	*	*
Echinodermata Ophiopluteus	*	*	*	*	*	*
Echinodermata Auricularia	*	*	*	*	*	*
Pisces	*	*	*	*	*	*
<i>Branchiostoma lanceolatum</i> juv.	*	*			*	*

DINAMIKA MEZOZOOPLANKTONA VZDOLŽ VZHODNE OBALE JUŽNEGA JADRANA

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POVZETEK

Avtorji so raziskovali časovno in prostorsko dinamiko mezozooplanktonske združbe vzdolž vzhodne obale južnega Jadranskega morja enkrat mesečno od oktobra 2012 do septembra 2013. Vzorce so pobirali z navpičnimi dvigi na dveh globinskih slojih treh postaj z uporabo Nansenove 200 μm planktonske mreže. Določili so skupno 141 holoplanktonskih taksonov, med katerimi so prevladovali raki ceponožci. Zaznali so velika nihanja celokupne abundance v časovni skali (od 181 os.m^{-3} oktobra do 1923 os.m^{-3} v maju). Združba mezozooplanktona se je v raziskanih slojih in sezonah značilno razlikovala. V globljih slojih in v zimskem času je prevladovala podpovršinska in mezopelagična favna, v toplejših mesecih pa so prevladovali značilne obalne jadranske vrste. Na podlagi primerjave z raziskavami s polovice prejšnjega stoletja so avtorji zaključili, da se v južnem Jadranu pojavlja stabilna mezozooplanktonska združba, na katero globalne spremembe manj vplivajo.

Ključne besede: raki ceponožci, sezonska nihanja, zooplankton, Sredozemsko morje

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