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GELATINOUS ZOOPLANKTON ASSEMBLAGES IN TEMPERATE COASTAL WATERS – SEASONAL VARIATIONS (GULF OF TRIESTE, ADRIATIC SEA)

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ABSTRACT

Gelatinous plankton composition, abundance, biomass and their seasonality was studied in the Gulf of Trieste (Adriatic Sea) over a yearly cycle. The most diverse gelatinous groups were Hydromedusae with 14 species, followed by Siphonophora (six species), Appendicularia (five species), Chaetognatha (two species), and Thaliacea (one species). In addition, the alien species Muggiaea atlantica, introduced into the Adriatic Sea in the early 90s, was for the first time recorded in the Gulf of Trieste. The carbon and nitrogen contents of gelatinous taxa varied from 7.4 to 34.4% and from 1.4 to 7.9% of dry weight, respectively. On a yearly basis, gelatinous plankton contributed less than 8% to total zooplankton dry weight with the highest contribution in late autumn. Cluster analysis (Bray-Curtis index) enabled us to distinguish three main gelatinous assemblages over an annual cycle.

Key words: gelatinous zooplankton, seasonal dynamics, coastal waters, Adriatic Sea

COMUNITÀ GELATINOSE ZOOPLANCTONICHE IN ACQUE TEMPERATE COSTIERE – VARIAZIONI STAGIONALI (GOLFO DI TRIESTE, MARE ADRIATICO)

SINTESI

La composizione, l'abbondanza, la biomassa e la stagionalità del plancton gelatinoso sono state studiate nel Golfo di Trieste (mare Adriatico) nell'arco di un ciclo annuale. Il gruppo gelatinoso più vario, che comprende 14 specie di idromeduse, è seguito da sifonofori (6 specie), appendicolarie (5 specie), chetognati (2 specie) e taliacei (1 specie). Nell'articolo viene segnalata per la prima volta la presenza nel Golfo di Trieste della specie aliena Muggiaea atlantica, introdotta in Adriatico negli anni novanta. I taxa gelatinosi hanno presentato variazioni nel contenuto di carbonio (da 7.4 a 34.4%) e azoto (da 1.4 a 7.9%) di peso secco. Su base annuale il plancton gelatinoso ha contribuito con meno dell'otto percento al peso secco totale dello zooplancton, con un picco massimo nel tardo autunno. La Cluster analysis (indice di Bray-Curtis) ha permesso di distinguere tre principali comunità gelatinose nell'arco di un ciclo annuale. Diverse idromeduse, sifonofori moderatamente abbondanti e poche appendicolarie hanno caratterizzato il periodo freddo pre-primaverile. Tunicati pelagici abbondanti (Thaliacea e Appendicularia), due specie di sifonofori e poche idromeduse hanno dominato il gruppo corrispondente ai mesi caldi. Una comunità planctonica con un'alta diversità e una moderata abbondanza ha invece rappresentato il terzo gruppo (novembre – gennaio).

Parole chiave: zooplancton gelatinoso, dinamica stagionale, acque costiere, mare Adriatico

INTRODUCTION

Gelatinous zooplankton forms a diverse pelagic group of animals belonging to different phyla (Cnidaria, Ctenophora, Mollusca, Chordata) with an important role in marine trophic webs that has been fully recognised only recently owing to their delicate bodies and the consequent difficulty of sampling, determination and laboratory experimentation. Despite their taxonomic diversity, these organisms share some common characteristics (Acuña, 2001) that define their life strategy: soft and transparent bodies without hard skeleton or thick muscles, high water content as a percentage of body mass, a relatively low carbon to dry mass ratio, and a rather large surface area relative to organic content (Larson, 1986). They are, with few exceptions, weak swimmers. These characteristics allow them a low maintenance metabolism and survival in a food diluted environment, but a rapid increase in size/numbers when food is plentiful. With few exceptions, gelatinous zooplankton show typical seasonality: they appear in masses in a given season while during the rest of the year they are rare or ab-

In spite of similarities among different gelatinous zooplankton, the trophic position of particular taxa are different and vary from grazers on picoplankton and nanoplankton (Thaliacea) to microzooplankton and larger mesozooplankton-feeders either through ambush (many Cnidaria, some Ctenophora) or as active predators (some Cnidaria and Ctenophora, pteropods, Chaetognatha). Due to a high growth rate and rapid generation time, gelatinous zooplankton may exert a significant grazing/predatory impact, seasonally outcompeting other planktonic grazers or predators. Results from several studies indicate that gelatinous organisms have important direct and indirect structuring impacts on the pelagic biodiversity (Batistić et al., 2004) and on the pelagic food web including the microbial part (Riemann et al., 2005; Malej et al., submit.). However, most of these observations are based on larger gelatinous organisms, such as Scyphomedusae and Ctenophora. Gelatinous organisms have few predators and are frequently considered as a "sink" within the pelagic food chain (CI-ESM, 2001), although data have accumulated recently on the utilization of gelatinous plankton as prey as well (Mianzan et al., 2001; Arai, 2005).

In coastal waters, the seasonality of gelatinous organisms has been related to changes in the physical characteristics and related trophic state of the pelagic environment (CIESM, 2001), *i.e.* the development of phytoplankton blooms which are replaced with oligotrophic conditions when nutrients are exhausted. The annual cycle of primary producers and their community structure in near-shore waters are generally controlled by nutrient inputs from freshwater inflow in conjunction with other environmental variables, such as temperature,

water column stratification, light availability and circulation (Valiela, 1995; Harding et al., 1999; Roman et al., 2005). In temperate waters, high biomass-high production periods are typically late winter-early spring and late summer-autumn, when phytoplankton is dominated by chain-forming diatoms. A mixture of nano-flagellates and small diatoms with lower biomass is characteristic of the transient period from spring to summer. The thermally stratified summer water column is characterized by high production-low autotrophic biomass and the prevalence of nano- and pico-sized phytoplankton. The described seasonality is also typical of the Gulf of Trieste, the northernmost part of the Adriatic Sea (Fonda Umani et al., 1995; Malej et al., 1995; Mozetič et al., 1998). Trophic regime shifts, which are associated with seasonal variations, are expected to be reflected in changes in gelatinous zooplankton assemblages (Mills, 1995). In this study, we explored the community structure, and the abundance and biomass of planktonic gelatinous assemblages in relation to variable environmental and trophic conditions in different seasons.

MATERIAL AND METHODS

A survey of environmental characteristics and plankton was carried out in the eastern part of the Gulf of Trieste at locations deeper than 20 m as part of the long-term monitoring programme (Mozetič & Lipej, 2002). The vertical structure of temperature, salinity and fluorescence was assessed using CTD fine-scale probe (University of Western Australia and a Sea-Tech inc. fluorometer).

Zooplankton samples were collected monthly by bottom to surface vertical tows using WP-2 net (net diameter 56 cm, 200 µm mesh) during 2001. Half of the zooplankton samples were used for dry weight (60 °C) and ash-free dry weight (500 °C) determination following standard procedures (Postel et al., 2000). From the other half of the samples, all gelatinous organisms were separated and identified, if possible, to the species level. All specimens were counted and the counts standardized to the number per m³. To obtain an objective description of the seasonal differences / similarities in gelatinous plankton assemblages, descriptive statistics was used. The Bray-Curtis similarity coefficient of (Field et al., 1983) and the linkage rule of the un-weighted pair group method using arithmetic averages (Sneath & Sokal, 1973) were applied. These data were then used to plot classification diagrams of percentage similarity.

For analyses of carbon and nitrogen content, gelatinous organisms were pooled into five main groups: Hydromedusae, Siphonophora, Chaetognatha, Appendicularia and Thaliacea. Pooled samples were dried and carbon and nitrogen were determined using Carlo Erba elemental analyser (Pella & Colombo, 1978); the results were expressed as % of dry mass.

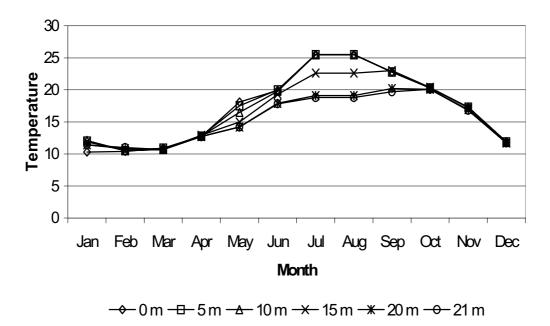
Čarna MILOŠ & Alenka MALEJ: GELATINOUS ZOOPLANKTON ASSEMBLAGES IN TEMPERATE COASTAL WATERS – SEASONAL VARIATIONS ..., 11-20

RESULTS

Physical environment

The water column was rather homogeneous in the winter months with temperatures ranging from 10.35 to 11.29 °C and salinities from 37.23 to 37.9 psu. In the top 2–5 m we recorded lower salinity values in March and July-August. In May, the surface layer warmed up to 18.20 °C, while the layer deeper than 15 m remained

colder (< 15 $^{\circ}$ C). The water column was well stratified from June to September with surface and bottom temperatures ranging between 23.0 and 25.92 $^{\circ}$ C and 17.65 and 20.49 $^{\circ}$ C, respectively. The thermocline and halocline were located at 15–18 m depth, creating a somewhat steep picnocline. The water column became more vertically homogeneous from October on with temperatures around 20 $^{\circ}$ C in October, 16 $^{\circ}$ C in November and 12 $^{\circ}$ C in December (Fig. 1).



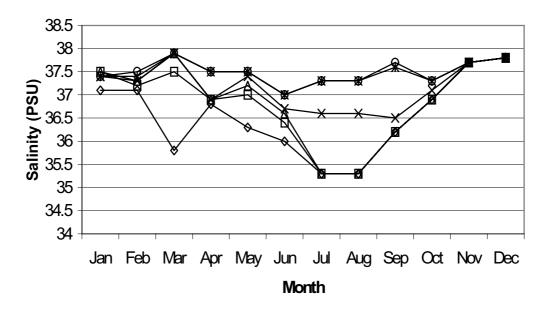


Fig. 1: Annual cycle of temperature (top) and salinity (bottom) at 5 depths during 2001. Sl. 1: Letni potek temperature (zgoraj) in slanosti (spodaj) na petih globinah leta 2001.

Tab. 1: Gelatinous plankton species collected during 2001 in the southeastern part of the Gulf of Trieste Tab. 1: Popis vrst želatinoznega planktona, najdenih l. 2001 v jugovzhodnem delu Tržaškega zaliva.

Phylum	Class	Order	Family	Genus	Species
Cnidaria	Hydroidea	Anthomedusae	Corynidae	Sarsia	S. gemmifera
					S. prolifera
				Dipurena	D. halterata
			Zancleidae	Zanclea	Z. costata
			Hydractiniidae	Podocoryne	P. carnea
					P. minuta
					P. minima
					P. spp.
		Leptomedusae	Campanulariidae	Obelia	O. spp.
				Phialidium	P. hemisphaericum
			Eirenidae	Helgicirrha	H. schultzei
			Eutimidae	Eutima	E. gracilis
		Trachymedusae	Rhopalonematidae	Aglaura	A. hemistoma
		Narcomedusae	Solmaridae	Solmaris	S. leucostyla
					S. vanhoeffeni
					S. spp.
	Siphonophora	Calycophorae	Hippopodiidae	Hippopodius	H. hippopus
				Vogtia	V. pentacantha
			Diphyidae	Muggiaea	M. kochi
					E. elongata
					M. atlantica
			Sphaeronectidae	Sphaeronectes	S. gracilis
Chaetognatha				Sagitta	S. setosa
					S. inflata
					S. spp.
	Appendicularia		Oikopleuridae	Oikopleura	O. dioica
					O. fusiformis
					O. longicauda
					O. vanhoeffeni
			Fritilariidae	Fritillaria	F. pellucida
		Thaliacea	Doliolida	Doliolum	D. gegenbauri

Gelatinous plankton composition, abundance and seasonal distribution

The most diverse group of gelatinous plankton (Tab. 1) were Hydromedusae with 14 species, followed by Siphonophora (six species) and Appendicularia (five species). Chaetognatha were represented by two species, although numerous juvenile individuals could not be identified to the species level. Only one species of Thaliacea was determined. While most other gelatinous taxa are holoplanktonic, among the Hydromedusae meroplanktonic species prevailed.

Total abundance of all gelatinous taxa ranged from a minimum of 60 ind/m³ in autumn (October) to two peaks with slightly over 1000 ind/m³ in June and over 1300 ind/m³ in September. Generally, a higher total abundance of gelatinous organisms was recorded in the

warmer part of the year (May-September) with only a few species present throughout the year.

The most numerous gelatinous group (Fig. 2) were Appendicularia with the single species *Oikopleura longicauda* reaching abundances between 327 and 518 ind/m³ in the summer months. In the same period, another Appendicularian (*Oikopleura fusiformis*) was quite abundant (38 to 159 ind/m³), while *Oikopleura dioica* was more numerous in the colder months (February-April, max. in March 199 ind/m³). Among Hydromedusae, the most abundant species was *Podocoryne minuta* (max. 24 ind/m³ in June), followed by *Podocoryne minima*, which was also more numerous during the warm months from April to September (max. 19 ind/m³). In contrast, peak abundances of *Obelia* spp. were registered in the cold period (December - March, max. 21 ind/m³ in December). Other, numerically less copious (<

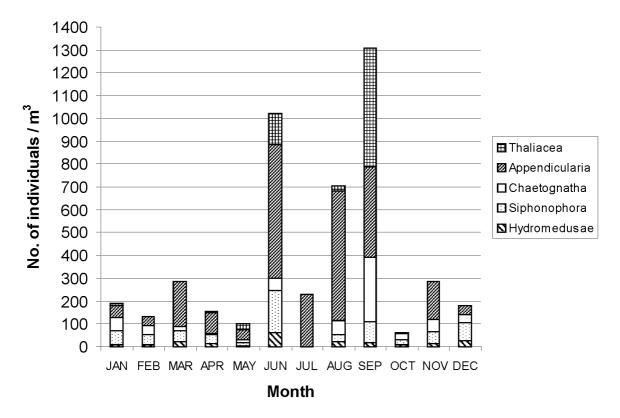


Fig. 2: Monthly abundance of the main gelatinous plankton groups during 2001 in the southeastern part of the Gulf of Trieste.

Sl. 2: Mesečne abundance skupin želatinoznega planktona leta 2001 v jugovzhodnem delu Tržaškega zaliva.

10 ind/m³) Hydromedusae species, were also associated with lower temperatures (November - April). Siphonophora, particularly two Muggiaea species, M. kochi and M. atlantica, were present throughout the year but showed two abundance peaks: in June (max. 84 ind/m³ for M. atlantica nectophore; max. 41 ind/m³ for M. kochi, nectophore) and September (max. 39 ind/m³ for M. kochi, gonophore). Chaetognatha were also present throughout the year, reaching maximal abundance in September (283 ind/m³), when individuals were almost entirely juvenile and thus not identified to the species level. Of the two species that were identified, Sagitta setosa was most abundant in June (16 ind/m³), whereas Sagitta inflata was registered only twice (in February and October). Doliolum gegenbauri, the only representative of Thaliacea, was found from March to November with peak abundance in September (518 ind/m³).

We used the Bray-Curtis similarity index to assess similarities among gelatinous assemblages in different months (Fig. 3). Using a similarity level of > 50 %, cluster analysis enabled us to distinguish three major groups of gelatinous assemblages over an annual cycle. Group B, typical of the cold period in transition to spring when the water column was vertically mixed (February-April), consisted of diverse Hydromedusae with species be-

longing to Leptomedusae, Trachymedusae and Narcomedusae, but very few Athomedusae. This period was also characterised by moderately abundant Siphonophora and Chaetognatha, while among Appendicularia only O. dioica was quite numerous. In contrast, group C, associated with the warm months and a vertically stratified water column (June, August-September), was characterized by the numerical dominance of Thaliacea (D. gegenbauri) and Appendicularia, the latter being represented by three species (O. longicauda, O. fusiformis and, to a lesser extent, Oikopleura vanhoeffeni), by important densities of Siphonophora that reached their annual peak during this period, and by an insignificant abundance of Hydromedusae, with the exception of Athomedusan *Podocoryne*. Group A comprised samples collected from November to January and was typified by rather high abundances of Siphonophora, which were represented by all six species registered in the studied area throughout 2001, by considerable abundances of Leptomedusae and Aglaura hemistoma, by moderate numbers of Appendicularia (O. longicauda, and, limited to this period of the year, Fritillaria pellucida). Certain months were distinguished at a similarity level of less than 50% (Fig. 3), and July was particularly isolated showing the lowest abundance of gelatinous organisms.

Bray-Curtis similarity index

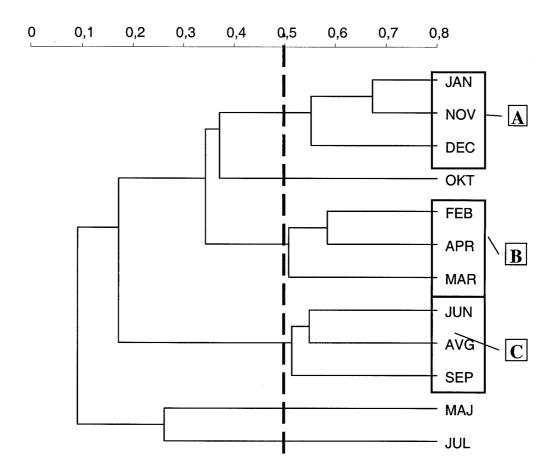


Fig. 3: Dendrogram of similarities (Bray-Curtis index) among gelatinous plankton assemblages (species list and abundance), collected in different months (see Tab. 1 for species list and Fig. 2 for abundances) of 2001. Sl. 3: Dendrogram podobnosti (Bray-Curtisov indeks) želatinoznega planktona (vrstna sestava in abundance) za različne mesece (glej Tab.1 za popis vrst in Sl. 2 za abundance) v letu 2001.

Biomass of gelatinous organisms and their contribution to total zooplankton biomass

Due to their small size, high water content and the consequent low dry mass per individual, organisms had to be pooled into groups for biomass analyses. Dry mass, carbon and nitrogen content, and C/N (atomic) ratios of Hydromedusae, Siphonophora (mainly *M. kochi)*, Chaetognatha (mainly *Sagitta* presumably *S. setosa* juv.) and Appendicularia (mainly *O. longicauda*) and Thaliacea (*D. gegenbauri*) are presented in Table 2. Carbon and nitrogen content varied widely: 7–34.4 and 1.4–7.9% of dry mass with the lowest values for Hydromedusae and the highest for Chaetognatha. C/N ratios were, in contrast, rather stable between 3.6 and 3.8, except for a slightly higher value for Hydromedusae.

Tab. 2: Carbon and nitrogen content and C/N ratio (atomic) of different gelatinous plankton groups.

Tab. 2: Vsebnost ogljika in dušika ter C/N razmerje (atomsko) različnih skupin želatinoznega planktona.

Group	% C	% N	C/N (atomic)
Hydromedusae	7.4	1.4	4.5
Siphonophora	34.3	7.9	3.7
Chaetognatha	34.4	7.9	3.7
Tunicata	31.9	7.4	3.6

The contribution of gelatinous organisms to total zooplankton biomass (on a dry weight basis) was below 8% throughout the year being the highest in November – December (Fig. 4) and above 5% also in June. Very low values (< 1%) were calculated for February and April – May. The contribution of different gelatinous taxa

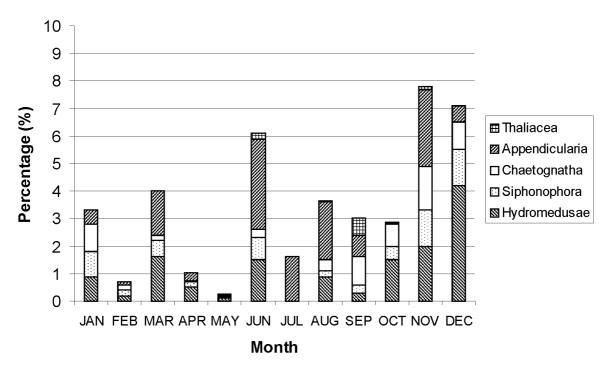


Fig. 4: Contribution of different gelatinous plankton groups to total zooplankton dry mass in different months of 2001 (expressed as %).

Sl. 4: Prispevki različnih skupin želatinoznega planktona k skupni suhi masi zooplanktona v različnih mesecih leta 2001 (izraženo kot %).

varied seasonally: Hydromedusae, Siphonophora and Chaetognatha contributed to a greater extent during the colder months, while Tunicates (Appendicularia and Thaliacea) contributed more during the warm season (Fig. 4).

DISCUSSION

Numbers of species for a particular taxonomic group of gelatinous plankton found during our one-year study are comparable to other studies in the Gulf of Trieste and, for most groups, to those from the wider northern Adriatic. For example, Benović et al. (2000) and Purcell et al. (1999) listed 14 Hydromedusae species in the northern Adriatic. The same number was found in this study. Rottini (1965) reported five Siphonophora species in the Gulf of Trieste, while our study showed six species, including the recently introduced species Muggiaea atlantica (Fig. 5) recorded in the Adriatic sea near Dubrovnik for the first time in 1995 (Gamulin & Kršinić, 2000; Kršinić & Njire, 2001). Moreover, Vogtia pentacontha (Fig. 6), a species characteristic for the Southern Adriatic and Mediterranean Sea, was found for the first time in the Gulf of Trieste. Two Chaetognatha species were found during our study, while Gamulin & Ghirardelli (1983) noted three species. In open northern Adriatic waters, Skaramuca (1983) found nine Appendicularian species compared to five found during our study in the Gulf of Trieste. In addition, seasonal patterns of the main gelatinous taxa observed during our study conformed to the general picture from previous reports with one exception: during July 2001, the abundance of all gelatinous organisms was unusually low. We explain such a decline in abundance to the mucilage phenomenon, which, in 2001, was limited to a rather short period in late June – early July (pers. obs.).

The seasonal presence of different gelatinous taxa and their grouping into two clear clusters could be related to their preferences for abiotic factors as well as to their trophic position. Two distinct seasonal assemblages (February - April and June - August - September) with transitions were found. However, many gelatinous organisms found in the Gulf of Trieste in 2001 seemed to be eurythermal and present over a rather wide temperature range. Species that clustered in group C (Fig. 3), typical of warm months and stratified water column, included the most abundant gelatinous organisms in our study, Appendicularia O. longicauda and O. fusiformis. Potential prey for Appendicularians consists of pico and nano-sized organisms, including auto- and heterotrophic bacteria (Lopez-Urrutia et al., 2003), although the clearing efficiency for picoplankton may be lower than that for larger prey (Scheinberg et al., 2005). A similar trophic position is occupied by doliolids that most likely rely on soft-walled food particles, such as flagellates (Paffenhöfer & Köster, 2005). Other abundant gelatinous

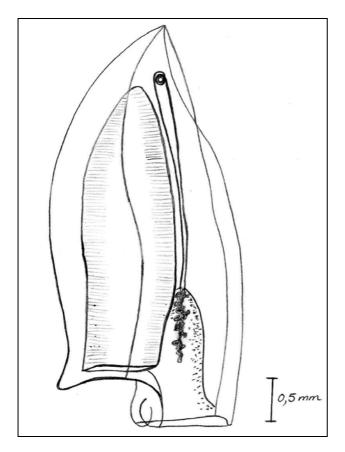


Fig. 5: Muggiaea atlantica (Diphyidae, Siphonophora) nectophore, a representative of the Atlantic fauna introduced in the Adriatic Sea in early 90-ties.

Sl. 5: Muggiaea atlantica (Diphyidae, Siphonophora)

SI. 5: Muggiaea atlantica (Diphyidae, Siphonophora) nektofor, predstavnica atlantske favne, vnešena v Jadransko morje v prvi polovici devetdesetih let.

organisms during the warm period included typical carnivorous organisms, such as *M. kochi* and *S. setosa*. The cold water group B, on other hand, was characterised by lower total abundances but more diverse gelatinous plankton, including hydromedusae that belonged to four subo. Anthomedusae, Leptomedusae, Tracymedusae and Narcomedusae, as well as Siphonophora and Chaetognatha. These organisms were traditionally viewed as top predators feeding on mesozooplankton. However, it has been recently shown that, for example, *Aglaura* was capable of feeding on prey ranging from greenpigmented protists to copepod nauplii (Colin *et al.*, 2005). The same authors predicted that many members of Hydromedusae could be expected to feed as omnivores.

Seasonal phytoplankton dynamics in the Gulf of Trieste in 2001 were rather typical of this region. Phytoplankton biomass and abundance reached their highest values in February (max. 4.99 µg Chl a/l, max. 2.4x10⁶ cells/l) due to a bloom of diatoms, particularly *Pseudo*-

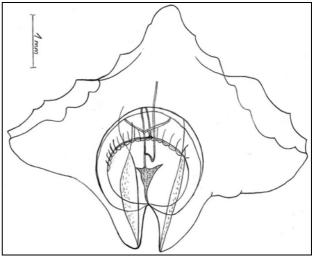


Fig. 6: Vogtia pentacantha (Hippopodiidae, Siphonophora) nectophore, species characteristic for deep waters found in the southern Adriatic.

Sl. 6: Vogtia pentacantha (Hippopodiidae, Siphonophora) nektofor, tipična globokomorska vrsta, značilna za južnojadransko kotlino.

nitzschia pungens, which constituted over 80% of the diatom population (Mozetič & Lipej, 2002). Gelatinous zooplankton are not likely to be able to prey efficiently on this chain-forming diatom, which is consistent with their low abundance (see Fig. 2) as well as their contribution to zooplankton dry mass (Fig. 4). Phytoplankton biomass was lower in late spring-summer (min. 0.36 µg Chl a/I, $< 3.0x10^5$ cells/I) and autumn ($< 2.0x10^5$ cells/I), when small flagellates, including coccolitophorids and silicoflagellates, prevailed. During this period, autotrophic and heterotrophic bacteria also reach their annual peak abundance (Turk et al., 2001, Fonda Umani & Beran, 2003). All these organisms represent potential prey for Appendicularians and doliolids, and indeed, from June to September pelagic tunicates reached their maximal abundance. Naked ciliates, copepod nauplia and copepodites, as other potential food sources for some gelatinous taxa, attained abundance peaks in June and September (Mozetič & Lipej, 2002), when in addition to pelagic tunicates, Hydromedusae, Siphonophora and Chaetognatha were also numerous.

Published data on the carbon and nitrogen content of gelatinous organisms are scarce, and different authors reported very different contents. Part of this variability might be attributed to bound water and the drying procedure. Also, the relative proportion of gonads, which are characterized by higher carbon and nitrogen contents compared to the rest of the gelatinous body (Larson, 1986), may influence results. Our data are within ranges published for different gelatinous taxa (Clarke *et al.*, 1992; Postel *et al.*, 2000). Values were on the low

Čarna MILOŠ & Alenka MALEJ: GELATINOUS ZOOPLANKTON ASSEMBLAGES IN TEMPERATE COASTAL WATERS – SEASONAL VARIATIONS ..., 11-20

side for Hydromedusae and higher for other gelatinous taxa, particularly for Chaetognatha, which Larson (1986) considered semi-gelatinous. Based on these values and their contribution to total zooplankton biomass on a dry weight basis (< 10 %), we could conclude that small gelatinous organisms played a minor trophic role during the period of our study, particularly during the months when copepods dominated the mesozooplankton community (winter – spring). Their role was more significant in the stratified water column, when pelagic tunicates preyed on pico and nano-sized autotrophs and hetero-

trophs that were abundant at that time. Carnivorous gelatinous groups and species (Siphonophora, Chaetognatha) were more important in late autumn.

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SEZONSKA NIHANJA ŽELATINOZNEGA ZOOPLANKTONA V OBALNIH VODAH (TRŽAŠKI ZALIV, JADRANSKO MORJE)

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POVZETEK

Avtorici poročata o sestavi, abundanci, biomasi in sezonskih nihanjih želatinoznega zooplanktona v teku letnega ciklusa v Tržaškem zalivu (Jadransko morje). Z največ vrstami so bile zastopane hidromeduze (14), ki so jim sledili cevkaši (6 vrst), repati plaščarji (5 vrst), ščetinočeljustnice (2 vrsti) in 1 vrsta salp. Tujerodna vrsta cevkašev Muggiaea atlantica je bila prvič registrirana za Tržaški zaliv. Vsebnost ogljika v suhi masi želatinoznih organizmov je nihala med 7,4 in 34,4%, dušika pa med 1,4 in 7,9%. Prispevek želatinoznih organizmov k suhi masi celotnega zooplanktona je bil najvišji pozno jeseni, vendar ni nikoli presegal 8%. Klastrska analiza (Bray-Curtisov podobnostni indeks) je nakazala grupiranje v tri skupine. Obdobje nizkih temperatur in prehod na pomlad opredeljuje pestra združba hidromeduz, zmerne abundance cevkašev in redki repati plaščarji. V združbi toplih mesecev številčno prevladujejo pelaški plaščarji (Thaliacea in Appendicularia), številni sta dve vrsti cevkašev, hidromeduze pa so maloštevilne. Značilnost tretje skupine (obdobje november – januar) so dokaj nizke abundance in vrstno pestra sestava želatinoznih organizmov.

Ključne besede: želatinozni zooplankton, sezonska dinamika, obalne vode, Jadransko morje

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