

# An invasion by *Muggiaea atlantica* CUNNINGHAM 1892 in the northern Adriatic Sea in the summer of 1997 and the fate of small copepods

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*The calyophoran siphonophore Muggiaea atlantica was found for the first time in the Adriatic Sea in February 1995 in the coastal region off Dubrovnik. At the beginning of summer 1997 in the shallow northern Adriatic it attained a maximum density of 450 nectophores m<sup>-3</sup> and 730 eudoxids m<sup>-3</sup>. During the time of the mass invasion of this allochthonous species of calyophore, a change in the structure, distribution and density of population of nauplii, copepodid stages and adult small copepods was observed.*

**Key words:** calyophores, mass invasion, small copepods, Adriatic Sea

## INTRODUCTION

*Muggiaea atlantica* is a representative of the Atlantic neritic fauna and is found mostly in the extreme western part of the Mediterranean Sea. Low densities of this species have been observed previously along the coast of Spain (WIRZ and BEYELER, 1954; ALVARIÑO, 1957; CERVIGON, 1958; VIVES, 1966), France (TRÈGOUBOFF, 1957; FURNESTIN, 1960) and in the Bay of Naples (IANORA and SCOTTO di CARLO, 1981). In the eastern Mediterranean basin, only a few specimens were found, especially off the coasts of Tunisia and Crete (BIGELOW and SEARS, 1937) and on the Levant coast (LAKKIS, 1971). The ATLANTIS II cruise in the open Mediterranean waters (GAMULIN and KRŠINIĆ, 1993a) collected a total of 175 nectophores, out of which the 80% in the westernmost part, while other specimens were collected at one location in the Tyrrhenian Sea. Just one specimen was found in the south-

ernmost part of the Ionian Sea (GAMULIN and KRŠINIĆ, 1993b).

Long-term, but sporadic, studies on calyophores have not found *Muggiaea atlantica* in the Adriatic Sea previously (GAMULIN, unpublished data). It was recorded in the Adriatic Sea for the first time in winter 1995, in its southern part. During 1996 it immigrated into the northern Adriatic where, in July 1997, it attained exceptionally high densities of both polygastric and sexual eudoxid stages. In this paper, we provide details regarding the changes observed in the small copepod community in the shallow northern part of the Adriatic, as a consequence of this exceptionally high population density of the species *M. atlantica*.

## MATERIAL AND METHODS

Zooplankton in the northern Adriatic Sea were sampled at three fixed stations (SJ101, SJ108 and SJ107), aboard the vessel RV VILA

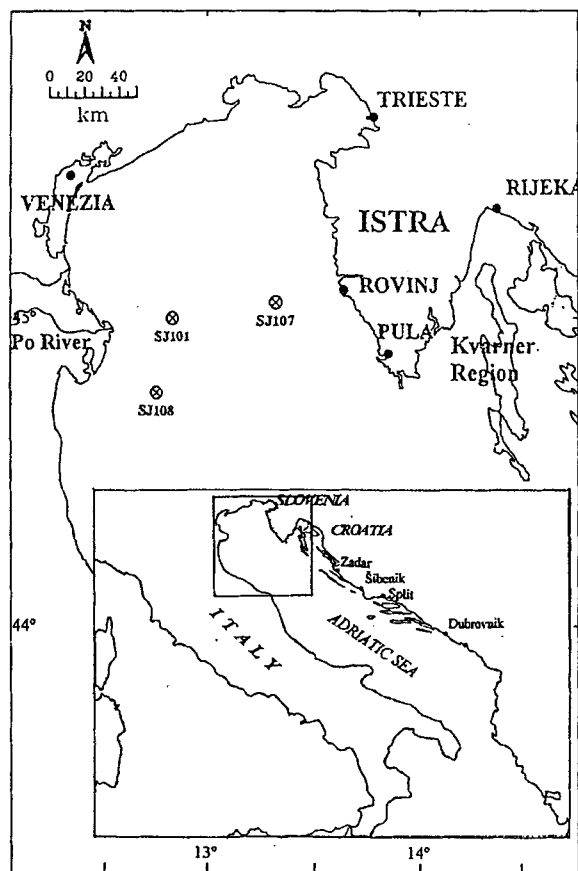


Fig. 1. Research area and sampling stations

VELEBITA of the Centre for Marine Research in Rovinj (Fig. 1).

This work gives details about research carried out during cruises in 1997: July 8 and 22, August 11, and September 1 and 23. The samples for the study on calycophores were taken by a vertical haul from the sea bottom to the surface with a NANSEN net 80 cm diameter and a mesh of 250  $\mu$ m. A sub-sample of 1/16 or 1/32 was analysed. The values were expressed as number of individuals per 1 m<sup>3</sup>. Samples for analyses of small copepods were taken at 1, 10, 20 m and 30m or 35m at SJ107 using a 5 l NISKIN bottle. All samples were preserved in a 2.5 % formaldehyde-seawater solution neutralized using C<sub>2</sub>CO<sub>3</sub>. In the laboratory, samples were sedimented until the original volume of 5 l was reduced to 20 ml, which took 72 h (KRŠINIĆ, 1980). The organisms were then counted by means of an inverted OLYMPUS IMT-2 microscope at magnifications of 100 and

400 x. Total samples were counted in a glass cell measuring 7 x 4.5 x 0.5 cm. Small copepod results are presented in terms of the number of specimens per litre. For correlation analysis, assemblages were logarithmically transformed ( $\log x+1$ ) to improve the normality of data (CASSIE, 1962).

### Study area and hydrography

The northern Adriatic basin is the northernmost part of the Mediterranean Sea. The basin is characteristically shallow (maximum depth 40 m), and is strongly influenced by rivers, particularly the Po, which accounts for about 60% of the total inflow of fresh water (CAVAZZONI GALAVERNI, 1972). In the western part of the northern Adriatic, which is affected by the inflow of Po water, extreme high values of phytoplankton production sometimes occur (DEGOBBIS, 1989). On the other hand, the eastern part of the northern Adriatic is influenced by oligotrophic water from the central and south Adriatic, particularly in late autumn and winter (ORLIĆ *et al.*, 1992). For details about the physical, chemical and production circumstances, see REVELANTE and GILMARTIN (1983); CEROVEČKI *et al.* (1991); FRANCO and MICHELATO (1992); BRANA and KRAJCAR (1995). In the last decade, in the region of the northern Adriatic, there have been frequent occurrences of marine snow or amorphous mucous aggregates (HERNDL and PEDUZZI, 1988; BOCHDANSKY and HERNDL, 1992).

The range, mean and SD for salinity and temperature in the period July - September are presented in Table 1.

During this period the water column was stratified, with a pronounced thermocline and halocline. The halocline was largely between 5 and 10 m depth. In the western stations, the thermocline was formed at a depth of between 5 and 10 m in July, while in August it was below 10 m. On the other hand, at the eastern station SJ107 as early as July, the thermocline was between 10 and 20 m depth. During the period from July 25 to August 11 gelatinous mucous aggregates were observed, first of all in the

Table 1. Range, mean  $\pm$  standard deviation of temperature ( $^{\circ}\text{C}$ ) and salinity (PSU) for the surface layer (0, 5, 10 m) and bottom layer (20, 30 and 35m for SJ107) from July 8 to September 23 1997 (Data CIM, Rovinj)

Stations		Surface layer		Bottom layer	
		T $^{\circ}\text{C}$	PSU	T $^{\circ}\text{C}$	PSU
SJ101	Min.	15.02	30.97	12.58	36.16
	Max.	27.40	37.03	19.83	37.51
	X	22.86	34.59	13.88	37.15
	SD	3.45	1.84	2.15	0.39
SJ108	Min.	16.79	25.72	12.38	36.72
	Max.	26.77	36.70	22.00	37.53
	X	23.33	33.74	15.05	37.17
	SD	3.01	2.93	3.27	0.32
SJ107	Min.	21.00	31.21	12.78	34.46
	Max.	26.29	35.96	20.74	37.63
	X	23.36	34.59	14.48	37.17
	SD	1.69	1.57	2.22	0.80

western, and then in the eastern part of the northern Adriatic (PRECALI, personal communication).

## RESULTS

### *Muggiaea atlantica* population structure

*Muggiaea atlantica* was found for the first time in the southern Adriatic at a station two nautical miles off Dubrovnik during the cruise of the RV BIOS in February 1995 in the 50 - 0 m layer. (0.6 nectophores  $\text{m}^{-3}$ ). Weekly sampling off Dubrovnik during the course of 1996 and 1997 indicated the almost continuous presence of this species.

A maximum density of 5 nectophores  $\text{m}^{-3}$  was detected in the surface layer on January 14, 1997.

Our data indicate that *Muggiaea atlantica* arrived in the northern Adriatic in 1996. Nectophore and eudoxid densities in January and March 1997 in the area of the northern Adriatic were similar to the values found around Dubrovnik. A mass invasion of this species was detected on July 8 throughout the northern

Adriatic. Maximum densities of 450 nectophores  $\text{m}^{-3}$  and 730 eudoxids  $\text{m}^{-3}$  were attained at station SJ101 (Fig. 2).

At the same station there were also high values on July 22, of 94 nectophores  $\text{m}^{-3}$  and 120 eudoxids  $\text{m}^{-3}$ . In August at stations SJ101 and SJ108 nectophores and eudoxids were absent. During September it was once again widespread, at all stations, with values of up to 24 nectophores  $\text{m}^{-3}$  and 45 eudoxids  $\text{m}^{-3}$ .

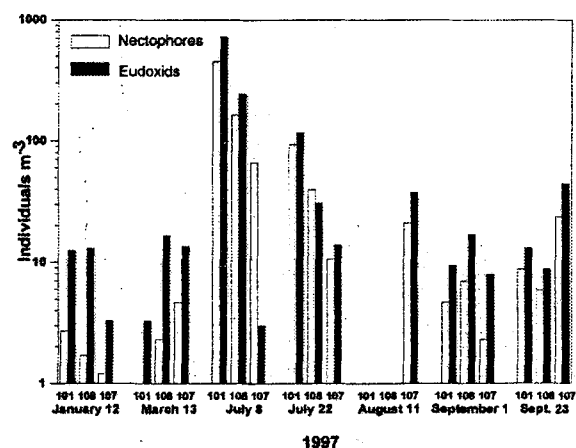


Fig. 2. *Muggiaea atlantica*, nectophore and eudoxid population density (No.  $\text{m}^{-3}$ ) from January to September 1997 at stations SJ101, SJ108 and SJ107

Copepod population structure

Nauplii

From the beginning of July to the end of September 1997 quite considerable differences

in the abundance and vertical distribution of nauplii among the stations were noted (Fig. 3).

At station SJ101, there were unusually low densities of nauplii throughout the summer. In the area of station SJ108 there was a high abundance of nauplii (465 ind l<sup>-1</sup>) at the surface on

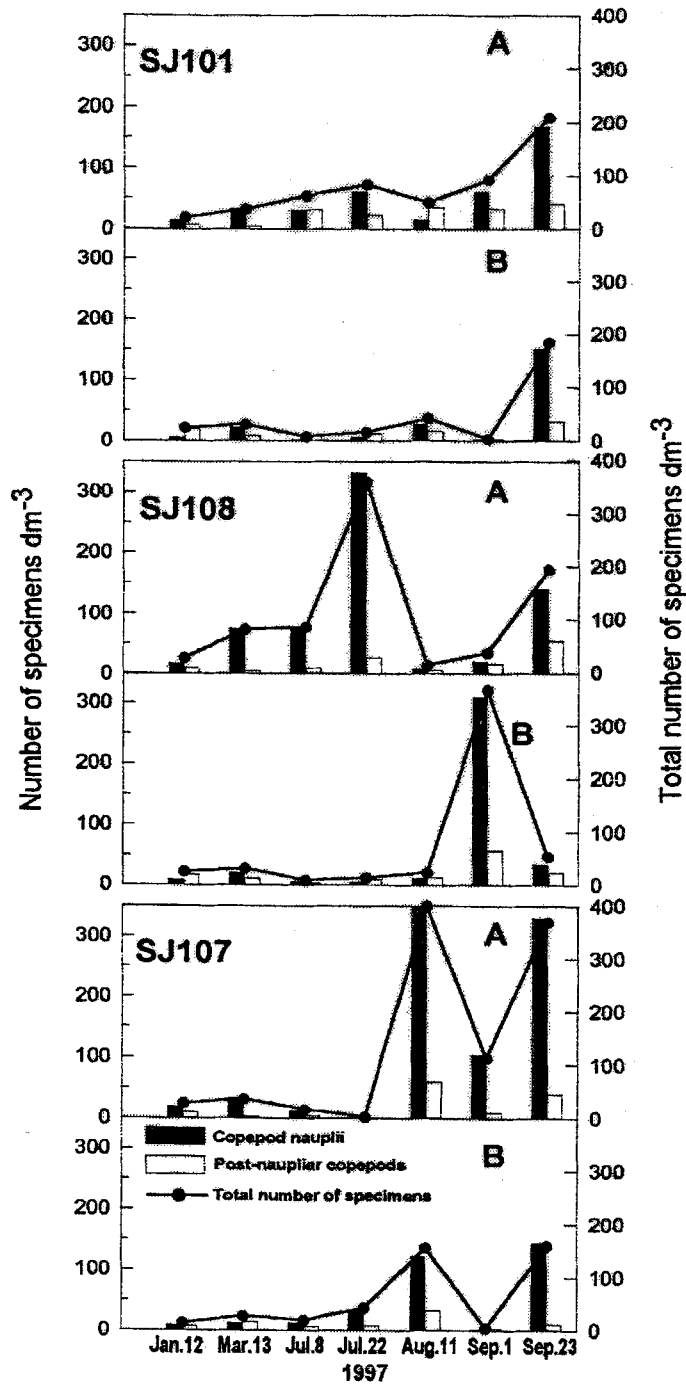


Fig. 3. Average population density of copepod nauplii, post-naupliar copepods and total number of specimens (No. dm<sup>-3</sup>); A. surface layer (1 and 10 m depth); B. bottom layer (20 m and 30 m or 35 m for SJ107) from January to September 1997

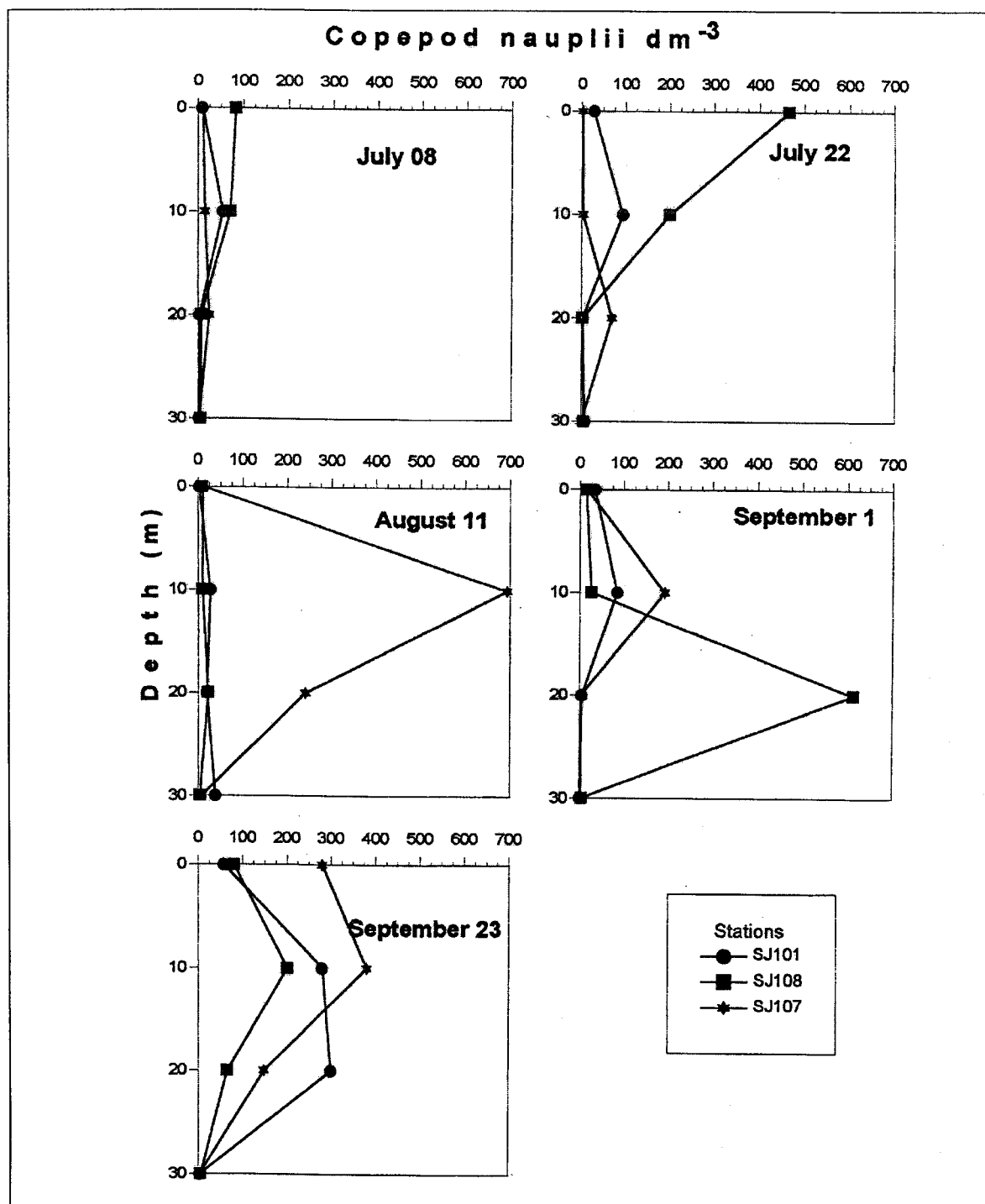


Fig. 4. Vertical distribution of nauplii population density from July 8 to September 23 1997

July 22 and 612 ind l<sup>-1</sup> at 20 m on September 1 (Fig. 4).

However, the density values in August fell to very low values, an average of 8 ind l<sup>-1</sup>. Naupliar density was very low at station SJ107

during the time of both July cruises, with mean values of only 5 to 11 ind l<sup>-1</sup>. In August, on the other hand, naupliar density was extremely high (690 ind l<sup>-1</sup> at 10 m). High values were also recorded at this station in September.

Copepodid stages and small adult copepods

Unlike nauplii, post-naupliar copepods increased in density in July during both cruises at station SJ101. At the same time they had

their lowest abundance at station SJ107. However, during later cruises an increased density of post-naupliar copepods was recorded at stations SJ108 and SJ107 (Figs 3 and 5). The maximum post-naupliar copepod density of 110 ind l<sup>-1</sup> was recorded at station SJ107

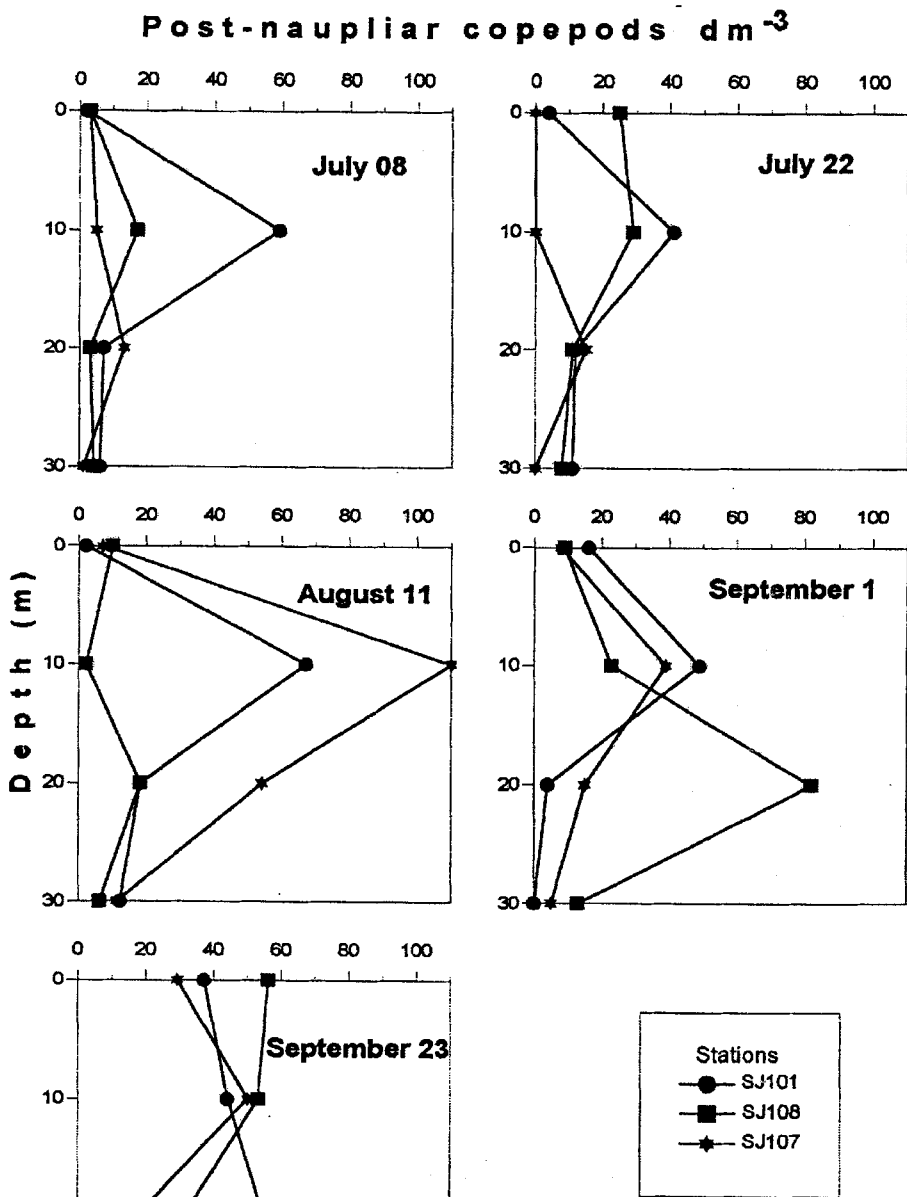


Fig. 5. Vertical distribution of postnaupliar copepods population density from July 8 to September 23 1997

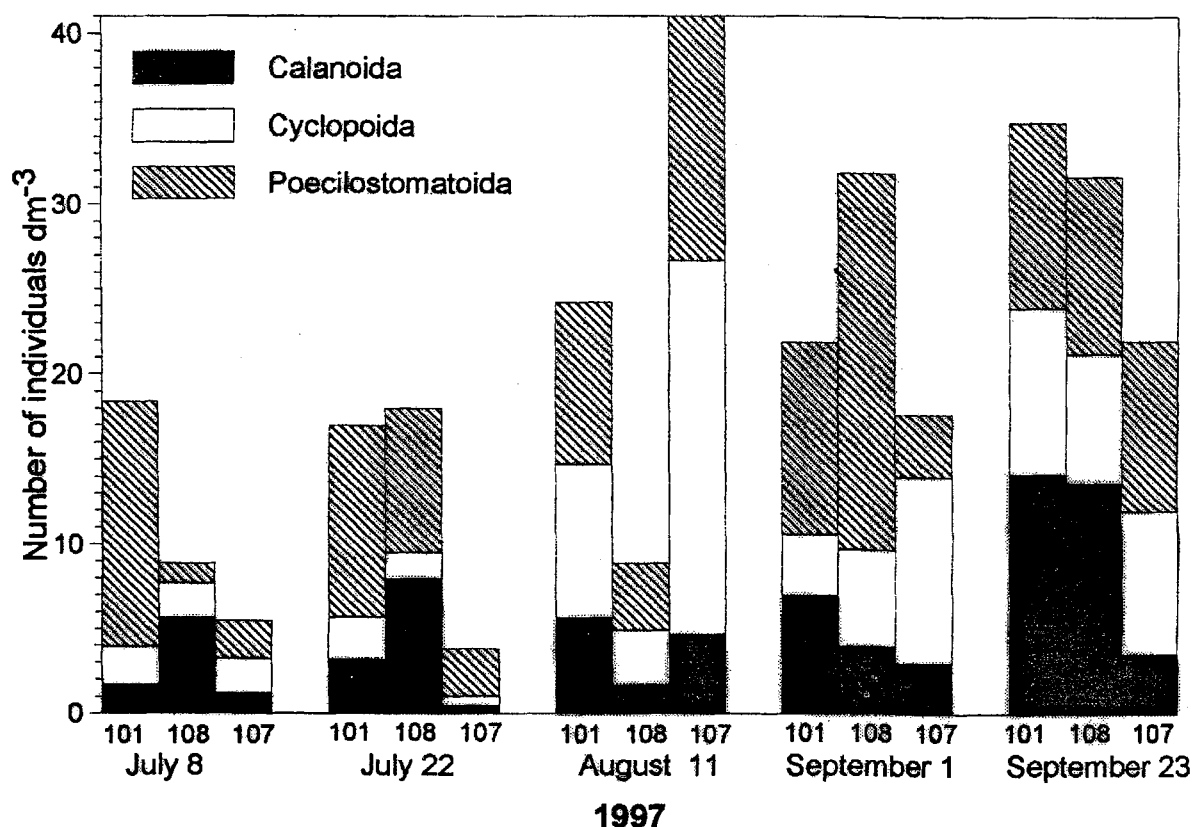


Fig. 6. Percentage of calanoid, cyclopoid and poecilostomatoid of the total number of post-naupliar copepods from July 8 to September 23 1997

in August at 10 m depth. In July, at station SJ101, copepodites and adults of the poecilostomatoid species *Oncaea waldemari* and *O. subtilis* were dominant, accounting for 66 to 79% of the total copepod population. In August and at the beginning of September at all stations, as well as poecilostomatoids, cyclopoids were considerably more abundant, with the dominant species being *Oithona nana*. It was only at the end of September that the proportion of calanoids in the total number of copepods increased (Fig. 6).

For the entire research period, only at station SJ107 was a significant correlation observed between the number of nauplii and all copepod groups ( $r=0.77$  between nauplii and calanoids;  $r=0.68$  between nauplii and

cyclopoids;  $r=0.89$  between nauplii and poecilostomatoids, d.f.=18,  $p<0.001$ ).

## DISCUSSION

Of the twenty-two species of calycophores identified from the Adriatic Sea, only six occur in the northern region. In this area the neritic species *Muggiaea kochi* is markedly dominant, contributing over 90% of the total number of nectophores (GAMULIN, 1979; ROTTINI and GAMULIN, 1969). During the seasonal cruises of the RV ANDRIJA MOHOROVIČIĆ between 1974 and 1976 (GAMULIN and KRŠINIĆ, 1993a), the highest density values, of 60 nectophores  $m^{-3}$ , were found during September-October 1974. Considerably lower densities of

nectophores were found in the western part in the area influenced by the River Po and other north rivers. There were particularly low numbers during the spring and summer period. In contrast, the invasion of *Muggiaea atlantica* in 1997 was established in the western part of the northern Adriatic during spring and early summer. In this period, a few specimens of the autochthonous species *Muggiaea kochi* were also recorded.

Suitable hydrographic conditions and the direction of the surface currents enabled the immigration of the species *Muggiaea atlantica* from the western part of the Mediterranean to the eastern part of the southern Adriatic during the winter-spring period of 1994/95. By direct measurements of the current at Otranto and in the southern Adriatic in 1994/1995, ascertained very prominent mean northward surface currents along the eastern shore of the Strait of Otranto (KOVAČEVIĆ *et al.* 1999).

Of particular importance is the fact that the species *Muggiaea atlantica*, after immigration into the Adriatic Sea, attained very high population density values in the northern part only. The mass appearance of incoming species and their role in the plankton of the northern Adriatic has been noted earlier: the medusa *Pelagia noctiluca* (MALEJ, 1989), the tintinnine species *Amphorides laackmanni* (KRŠINIĆ and PRECALI, 1996).

High densities of *Muggiaea atlantica* nectophores ( $218 \pm 156 \text{ m}^{-3}$ ) and eudoxids ( $1207 \pm 596 \text{ m}^{-3}$ ) were found by PUGH and BOXSHALL (1984) off the northwest coast of Africa. GREVE (1994) noted an invasion of this species during summer 1989 in the area of the German Bight. The abundance of the species reached up to 500 colonies  $\text{m}^{-3}$  in August. According to that author, the invasion had a great impact on in the pelagic ecosystem. Predation on small copepods caused a reduction of the grazing pressure on phytoplankton, enabling the growth of algae populations.

In the northern Adriatic at the time of the highest density of polygastric colonies and eudoxids in July 1997, very low densities of copepod nauplii were recorded. At the same

time, higher values of the total number of post-naupliar copepods, though with a considerably increased contribution of copepods of the genus *Oncaea*, were recorded. Oncaeid copepods played an important role in the total copepod number during the whole of that summer period. In earlier research, *Oncaea* copepods had been present in the plankton of the northern Adriatic in the autumn and winter period, while during the summer, calanoid and cyclopoid copepods dominated (HURE and SCOTTO di CARLO, 1969; HURE *et al.*, 1980; KRŠINIĆ, 1995; HURE and KRŠINIĆ, 1998). Low population density values for nauplii and postnaupliar copepods of calanoids and cyclopoids can be linked with increased grazing pressures from the species *M. atlantica*. According to PURCEL (1982) *Muggiaea atlantica* consumed mainly small calanoid copepods, nauplii and copepodid stages. The daily prey consumption was estimated to be 5.5 to 10.5 prey siphonophore<sup>-1</sup> day<sup>-1</sup>. On the other side, it may be assumed that the increase of oncaeid density plays a significant role in the processes of calycophorids decomposition. It is known that oncaeid copepods because of their feeding behavior show a high frequency of association with larger gelatinous organisms (OHTSUKA and KUBO, 1991; GO *et al.*, 1998).

Accordingly, the abundance and spatial distribution of nauplii in 1997 is considerably different from that in previous years, during increased eutrophication or the mass appearance of gelatinous macroaggregates (REVELANTE and GILMARTIN, 1983; REVELANTE *et al.*, 1985; KRŠINIĆ *et al.*, 1988; KRŠINIĆ, 1995). Almost as a rule, nauplii are most numerous in the warm part of the year, but are much more abundant in the western stations in the area affected by the water of the River Po and increased production (SJ101, SJ108). On the other hand, in the years of the mass appearance of gelatinous macroaggregates (1989, 1991) the characteristic naupliar maximum in the open waters of the northern Adriatic was absent. During the summer months of 1997 a horizontal shift of the centre of increased naupliar density and of the total number of post-naupliar cope-



pods away from the western station SJ108 towards the eastern station SJ 107 and back to station SJ108 was registered. Owing to more frequent sampling we were able to determine a horizontal movement of copepod patchiness which could be linked to the currents in that region during the summer months (ORLIĆ *et al.*, 1992; BRANA and KRAJCAR, 1997). In addition, the determined distributions show the gradual process of the regeneration after invasion by *M. atlantica* in the open waters of the northern Adriatic.

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## REFERENCES

- ALVARIÑO, A. 1957. Estudio del zooplancton del Mediterráneo occidental. Bol. Inst. Español Oceanogr., 81: 1-26.
- BIGELOW, H. B. and M. SEARS. 1937. Siphonophorae. Report on the Danish Oceanographical Expedition 1908-1910, to the Mediterranean and adjacent seas 2 (H2): 1-144.
- BOCHDANSKY, A.B. and G. HERNDL. 1992. Ecology of amorphous aggregations (marine snow) in the Northern Adriatic Sea. III. Zooplankton interactions with marine snow. Mar. Ecol. Prog. Ser., 87: 135-146.
- BRANA, J. and V. KRAJCAR. 1995. General circulation of the northern Adriatic Sea: Results of long-term measurements. Estuar. coast. Shelf Sci., 40: 421-434.
- CASSIE, R. M. 1962. Frequency distribution models in the ecology of plankton and other organisms. J. Animal Ecol., 31: 65-92.
- CAVAZZONI GALAVERNI, S. 1972. Acque dolci nell'Adriatico settentrionale fino alla latitudine di 44°47'. CNR, Laboratorio per lo Studio della Dinamica delle Grandi Masse. Venezia, Rapporto Tecnico No. 27, 31pp.
- CEROVEČKI, L., Z. PASARIĆ, M. KUZMIĆ, J. BRANA and M. ORLIĆ. 1991. Ten-day variability of the summer circulation in the Northern Adriatic. Geofizika, 8: 67-81.
- CERVIGON, F. 1958. Contribución al estudio de los sifonóforos de las costas de Castellón (Mediterráneo Occidental). Inv. Pesqu., 12: 21-47.
- DEGOBBIS, D. 1989. Increased eutrophication of the Northern Adriatic Sea. Second Act. Mar. Pollut. Bull., 20: 452-457.
- FRANCO, P. and A. MICHELATO. 1992. Northern Adriatic Sea: oceanography of the basin proper and the western coastal zone. Sci. Total Environ., (Suppl.): 35-62.
- FURNESTIN, M. L. 1960. Zooplankton du Golfe du Lion et de cte orientale de Corse. Rev. Trav. Inst. Pêches Marit., 24: 153-252.
- GAMULIN, T. 1979. Zooplankton istočne obale Jadranskog mora. Acta biologica, 8: 177-270.
- GAMULIN, T. and F. KRŠINIĆ. 1993a. Distribution and abundance of Calycophores (Siphonophora, Calycophorae) in the Mediterranean and Adriatic Sea. P.S.Z.N.I: Mar. Ecol., 14: 97 - 111.
- GAMULIN, T. and F. KRŠINIĆ. 1993b. On the occurrence of Calycophorae (Siphonophora) in the southern Adriatic and Tyrrhenian Sea: a comparison of the annual cycles off Dubrovnik and Naples. J. Plankton Res., 15: 855-865.
- GO, Y.B., B.C. OH and M. TERAZAKI. 1998. Feeding behavior of the poecilostomatoid

- copepods *Oncaea* spp. on chaetognaths. Journal of Marine Systems, 15: 475-482.
- GREVE, W. 1994. The 1989 German Bight invasion of *Muggiaea atlantica*. ICES J. Mar. Sci., 51: 355-358.
- HERNDL, G.J. and P. PEDUZZI. 1988. The ecology of amorphous aggregations (marine snow) in the Northern Adriatic Sea: I. General considerations. P.S.Z.N.I.: Mar. Ecol., 9: 79-90.
- HURE, J. and B. SCOTTO di CARLO. 1969. Copepodi pelagici dell'Adriatico settentrionale nel periodo gennaio-dicembre 1965. Pubbl. Staz. Zool. Napoli, 37:173-195.
- HURE, J. and F. KRŠINIĆ. 1998. Planktonic copepods of the Adriatic Sea. Spatial and temporal distribution. Nat. Croat., 7 (suppl. 2): 1 - 135.
- HURE, J., A. IANORA and B. SCOTTO di CARLO. 1980. Spatial and temporal distribution of copepod communities in the Adriatic Sea. J. Plankton Res., 2: 295-316.
- IANORA, A. and B. SCOTTO di CARLO. 1981. The distribution and annual cycles of Siphonophora Calycophora in the Gulf of Naples and adjacent waters. Arch. Oceanogr. Limnol., 20: 51-65.
- KOVAČEVIĆ, V., M. GAČIĆ and P.M. POULAIN. 1999. Eulerian current measurements in the Strait of Otranto and in the Southern Adriatic. J. Mar. Syst., 20: 255-278.
- KRŠINIĆ, F. 1980. Comparison of methods used in micro-zooplankton research in neritic waters of the eastern Adriatic. Nova Thalassia, 4: 91-106.
- KRŠINIĆ, F. 1995. Changes in the microzooplankton assemblages in the northern Adriatic Sea during 1989 to 1992. J. Plankton Res., 17: 935-953.
- KRŠINIĆ, F. and R. PRECALI. 1996. On the occurrence of oceanic tintinnines with particular consideration of the species *Amphorides laackmanni* (Jrgensen, 1924), (*Ciliophora*, *Oligotrichida*, *Tintinnina*) in the Northern Adriatic Sea. P.S.Z.N.: Mar. Ecol., 18: 67-81.
- KRŠINIĆ, F., D. MUŠIN and M. RUDENJAK-LUKENDA. 1988. Microzooplankton and eutrophication of the Northern Adriatic. Pomorski Zbornik, 26: 601-612 (in Croatian).
- LAKKIS, S. 1971. Contribution à l'étude du zooplancton des eaux libanaises. Mar. Biol., 11: 138 - 148.
- MALEJ, A. 1989. Behaviour and trophic ecology of the jellyfish *Pelagia noctiluca* (Forsk., 1775). J. Exp. Mar. Biol. Ecol., 126: 259-270.
- OHTSUKA, S. and N. KUBO. 1991. Larvaceans and their houses as important food for some pelagic copepods. Proceeding of the Forth International Conference on Copepoda. Bulletin of Plankton Society of Japan. Spec. Vol.: 535-551.
- ORLIĆ, M., M. GAČIĆ and P.E. LA VIOLETTE. 1992. The currents and circulation of the Adriatic Sea. Oceanologica Acta, 15: 109-124.
- PUGH, P. R. and G. A. BOXSHALL. 1984. The small-scale distribution of plankton at a shelf station off the northwest African coast. Continental Shelf Research, 3: 399-423.
- PURCELL, J. 1982. Feeding and growth of the siphonophore *Muggiaea atlantica* (Cunningham, 1893). J. Exp. Mar. Biol. Ecol., 62: 9-54.
- REVELANTE, N. and M. GILMARTIN. 1983. Microzooplankton distribution in the Northern Adriatic Sea with emphasis on the relative abundance of ciliated protozoans. Oceanologica Acta, 6: 407-415.
- REVELANTE, N., M. GILMARTIN and N. SMODLAKA. 1985. The effects of Po river induced eutrophication on the distribution and community structure of ciliated protozoan and micrometazoan populations in the northern Adriatic Sea. J. Plankton Res., 7: 461-471.
- ROTTINI, L. and T. GAMULIN. 1969. Distribuzione dei sifonofori in Adriatico a nord della trasversale Fano-Lussino. Boll. Pesca, Piscics. Idrobiol., 24: 79-89.

- TRÉGOUBOFF, G. 1957. Siphonophores. in: Trégouboff & Rose (Editor). Manuel de Planctonologie Méditerranéenne. Centre National de la Recherche Scientifique Paris, Tom I, 587 pp, Tom II, 207 pls.
- VIVES, F. 1966. Zooplankton nerítico de las aguas de Castellón. (Mediterráneo occidental). Inv. Pesqu., 30: 49-166.
- WIRZ, K. and M. BEYELER. 1954. Recherches sur le zooplancton de surface dans l'Ouest de la Méditerranéenne Occidentale en Juin et Juillet 1952. I. Partie générale. Résultats des Campagnes du "Pr. Lacaze Duthiers" sur les côtes d'Algérie (Juin-Juillet 1952). Vie et Milieu, Suppl. 3: 96-114.

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## **Masovna pojava vrste *Muggiaea atlantica* CUNNINGHAM 1892 u sjevernom Jadranu za vrijeme ljeta 1997. godine i sudbina malih kopepoda**

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### **SAŽETAK**

Vrsta kalikofora *Muggiaea atlantica* je prvi put nađena u Jadranskom moru tijekom veljače 1995. godine u obalnom moru Dubrovnika. Početkom ljeta 1997. godine u otvorenom dijelu sjevernog Jadrana dostiže maksimalnu gustoću nektofora (450 n m<sup>-3</sup>) i eudoksija (730 e m<sup>-3</sup>). U vrijeme masovne pojave ove kalikofore utvrđena je promjena sastava, raspodjele i gustoće populacije nauplija, kopepodita i odraslih malih kopepoda.