

ORIGINAL ARTICLE

Did the alien calyphorophoran *Muggiaea atlantica* outcompete its native congeneric *M. kochi* in the marine lakes of Mljet Island (Croatia)?

Mirna Batistić¹, Davor Lučić¹, Marina Carić¹, Rade Garić¹, Priscilla Licandro² & Nenad Jasprica¹

¹ Institute for Marine and Coastal Research, University of Dubrovnik, Dubrovnik, Croatia

² Sir Alister Foundation for Ocean Science, The Laboratory, Plymouth, UK

Keywords

Adriatic Sea; life cycle; marine lakes; *Muggiaea atlantica*; Zooplankton.

Correspondence

Mirna Batistić, Institute for Marine and Coastal Research, University of Dubrovnik, Kneza Damjana Jude 12, HR-20000 Dubrovnik, Croatia.
E-mail: mirna.batistic@unidu.hr

Accepted: 2 October 2012

doi: 10.1111/maec.12021

Abstract

The calyphorophoran siphonophore *Muggiaea atlantica* was recorded for the first time in the marine lakes of Mljet Island (South Adriatic) in 2001. The presence of *M. atlantica* in such semi-enclosed environments provided a unique opportunity to describe its life cycle based on *in situ* observations of the annual variability of its asexual nectophore stage, sexual eudoxid stage (produces gonophores) and calyconula larvae. *Muggiaea atlantica* was present the whole year in the Malo jezero (Small Lake, SL), where it was actively reproducing between May and September 2001, with a maximum density of gonophores in May (141 gonophores m⁻³) and nectophores and larvae in June (37 nectophores m⁻³ and 80 larvae m⁻³). Higher temperatures below the thermocline (average 14.5–15.6 °C), and the availability of prey (e.g. small copepods, chaetognaths and bivalve larvae) were the main environmental factors related to successful reproduction of *M. atlantica* in SL. In the Veliko jezero (Great Lake, GL) nectophores and gonophores of *M. atlantica* were found in low numbers, mainly in the upper 20 m, between September and November 2001 and no larvae were recorded. In 2001, *Muggiaea kochi*, the sole calyphorophoran siphonophore previously reported in the GL, was not recorded in the Mljet lakes. We hypothesize that the cold (<13 °C) conditions over winter of 2000/2001 were not suitable for the warm-temperate *M. kochi* and may have favoured its cold-temperate congener, *M. atlantica*, which has progressively colonized the southern Adriatic since the mid-1990s.

Introduction

Prior to the 1980s, *Muggiaea atlantica*, a representative of the Atlantic neritic fauna, was found most frequently in the westernmost part of the Mediterranean (Ianora & Scotto di Carlo 1981; Gamulin & Kršinić 1993). Expansion of its range to the Northwestern Mediterranean, with increased abundance, was observed from the mid-1980s (Gili *et al.* 1988; Licandro & Ibanez 2000). *Muggiaea atlantica* was first recorded in the Adriatic Sea in 1995 (Batistić 1999; Gamulin & Kršinić 2000), a year in which the advection of West Mediterranean/Atlantic water into the Adriatic Sea was related to the anticyclonic circulation

in the Ionian Sea (Civitarese *et al.* 2010). A shift in dominance among Adriatic calyphorophorans was noted from 1996, with *Muggiaea kochi* being replaced by *M. atlantica* (Kršinić & Njire 2001; Batistić *et al.* 2007). The geographical expansion of *M. atlantica* and decrease of *M. kochi* was triggered by thermohaline circulation changes that occurred in the Mediterranean and Adriatic Sea in the last two decades, probably under the forcing of large-scale climate oscillations (Licandro & Ibanez 2000; Batistić *et al.* 2007; Licandro *et al.* 2012).

The present study is based on data collected in the two marine lakes on the island of Mljet between December 2000 and December 2001. The colonization of this

semi-enclosed marine environment by *M. atlantica* provided a good opportunity to investigate its life cycle by following the annual variability of the asexual and sexual stage and calyconula larvae. Such data are quite scarce and would be impossible to derive should *M. atlantica* co-occur with the congeneric *M. kochi*, due to morphologically indistinguishable eudoxids and larvae. Another aim of this study was to identify the main abiotic and biotic factors that influence development of *M. atlantica* in the lakes, to allow a better understanding of its recent establishment in the Adriatic and Mediterranean Sea, particularly in relation to hydroclimatic changes. A final goal was to assess the impact of this novel species on the zooplankton community of the lakes, particularly the impact on native calycophoran fauna.

Study area

The Island of Mljet, situated in the South Adriatic off Dubrovnik, is directly exposed to the incoming Ionian Sea current (Zore-Armanda *et al.* 1991). Two seawater lakes, Veliko jezero (Great Lake, GL) and Malo jezero (Small Lake, SL), are situated in the western part of the island (Fig. 1). Both lakes have been part of a national park for more than 40 years, thus representing an excellent study site without direct human impact. The lakes are naturally formed karstic depressions that were filled with seawater during the holocene ingress of the Adriatic Sea, about 5000–7000 years ago (Schmidt 1993). The Great Lake has a surface area of 1.45 km² and maximum

depth of 46 m, and the Small Lake has a surface area of 0.25 km² and maximum depth of 29 m. Tidal currents are the main factor driving water exchange between the open sea and the lakes. This exchange is limited owing to the small tidal range and the shallow depth of the straits connecting the Soline Channel to GL (10 m width, 2.5 m depth) and GL to SL (3 m width, 0.6 m depth) (Fig. 1). The lakes are as much as 2–3 °C colder than the open sea during winter and as much as 4 °C warmer during summer, with surface temperatures as high as 28 °C and a strong thermocline (up to 4 °C m⁻¹) at 10–20 m depth (Vilibić *et al.* 2010). Compared with an earlier investigation that found salinity restricted to values of 35–37 (Buljan & Špan 1976), salinities greater than 37 have been found since the 1990s (Benović *et al.* 2000; Malej *et al.* 2007).

Phytoplankton abundance and structure are similar to those in the neighboring open Adriatic (Jasprica *et al.* 1995). The maximum microphytoplankton abundance in GL (4.0×10^4 cells l⁻¹) and SL (5.9×10^4 cells l⁻¹) was in summer, whereas the maximum nanophytoplankton abundance in GL (4.5×10^6 cells l⁻¹) and SL (2.2×10^6 cells l⁻¹) was in winter and summer, respectively (Jasprica *et al.* 1995).

Material and Methods

Monthly sampling was carried out from December 2000 to December 2001 in both Veliko jezero (GL) and Malo jezero (SL) (Fig. 1).

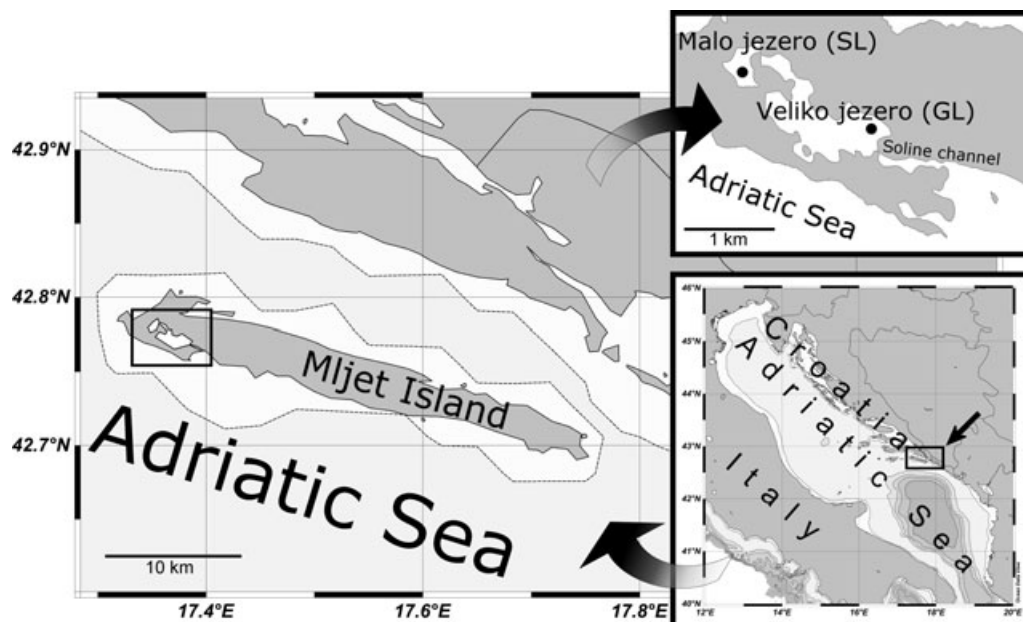


Fig. 1. Map of the marine lakes Veliko jezero (GL) and Malo jezero (SL) on Mljet Island. Black points indicate sampling sites.

Zooplankton samples were collected using a Nansen net (40-cm diameter) fitted with a 125- μ m mesh. One vertical haul was done from the bottom to the surface in SL (0–25 m) due to the relatively shallow depth; two separate layers (0–20 m and 20 m to the bottom) were sampled in GL. Samples were preserved in a buffered 2.5% formalin-seawater solution. Hydrographic parameters and chlorophyll *a* (Chl *a*) concentration were measured in water samples taken with a 5-l Niskin bottle every 5 m from the surface to the bottom. Salinity was determined using the standard titration method (Grasshoff 1983), temperature with an inverted thermometer, and dissolved oxygen using the Winkler method. Oxygen saturation (O_2/O_2') was calculated from the solubility of oxygen in seawater as a function of temperature and salinity (Weiss 1970; UNESCO 1973). Chl *a* was determined from 0.5-l sub-samples filtered through Whatman GF/F glass-fiber filters and stored at -20°C . Filtered samples were homogenized and extracted in 90% acetone for 24 h at room temperature (Strickland & Parsons 1972). Chl *a* was then measured fluorometrically with a Turner TD-700 Laboratory Fluorometer calibrated with pure Chl *a* (Sigma-Aldrich, Taufkirchen, Germany).

Taxonomic identification and counting of net zooplankton were performed with a Zeiss stereomicroscope at 25 \times and 40 \times . The life cycle of the diphyid siphonophore *M. atlantica* was investigated by following the annual variability of the asexual and sexual stages, and the calyconula larvae. Nectophore count was used to estimate the asexual stage abundance. Gonophores, released by sexual stage eudoxids, were counted to estimate the reproductive activity. Eudoxids live autonomously, themselves budding several gonophores. The abundances of the different stages (Fig. 2) were counted in the whole sample and then converted into numbers per m^3 . These stages were determined according to Moser (1925), Russell (1938) and Bouillon *et al.* (2004). Hydromedusae, pteropoda, bivalvia larvae, cladocera, ostracoda, copepoda (divided into calanoid, poecilostomatoid, cyclopoid and harpacticoid), chaetognatha, and appendicularia were also counted as a fraction of the samples varying between 1/4 and 1/32 of the original sample volume. The abundance of those groups was then converted to number of specimens per cubic meter (ind. m^{-3}).

Principal component analysis (PCA) was carried out on a matrix composed of 13 monthly abundances of nectophores and gonophores of *M. atlantica* for GL and SL. The interpretation of the first (PC1) and second (PC2) principal components, which together accounted for 91% of the total variance, involved seven environmental descriptors (water temperature, salinity, oxygen

and chlorophyll *a* concentration integrated from the surface to bottom depth; temperature above and below the thermocline; mixed layer depth) and 11 biological descriptors (the plankton groups specified in the preceding paragraph). Only those descriptors that showed the greatest correlation to the PC1 and PC2 (i.e. Pearson correlation >0.5) are presented here.

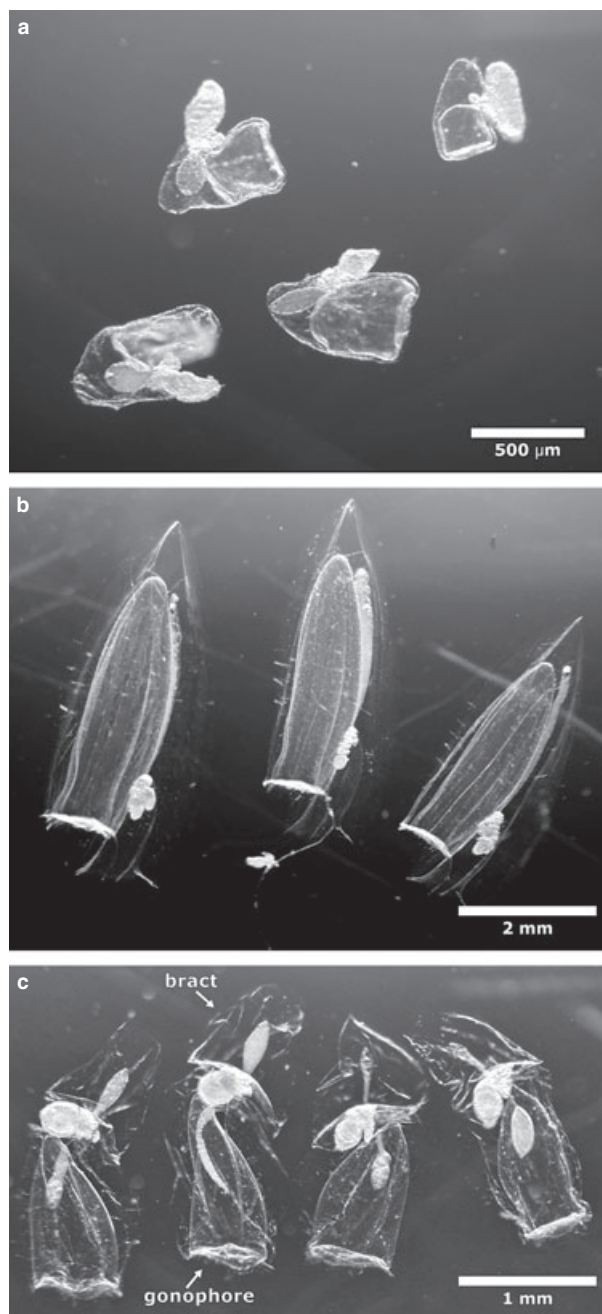


Fig. 2. *Muggiaea atlantica*: calyconula larvae (a), nectophores (b), eudoxids (c).

Results

Hydrography

The temperature in Veliko jezero (GL) ranged from 11.1 °C near the bottom in December 2000 to 26.4 °C at the surface in August 2001 (Fig. 3). In Malo jezero (SL) temperatures ranged from the 9.1 °C near the bottom in December 2001 to 28.3 °C at the surface in July 2001 (Fig. 3). Temperature was evenly distributed throughout the water column in winter in both lakes (Fig. 3, Table 1). Inverse stratification occurred only in February in SL in the upper 5 m layer, owing to faster cooling at the surface (see also Buljan & Špan 1976). A thermocline was well established between June and September, with a maximum temperature difference of 1.4 °C m⁻¹ in August (SL) and September (GL). In June, July and August the thermocline in GL was at 15–20 m and in SL at 10–15 m. In both lakes the thermocline was deeper in September (Table 1). The temperature below the thermo-

cline was generally 2 °C lower in GL than in SL (Table 1).

Salinity varied between 32.99 and 38.82 (yearly average = 38.00 ± 1.05) in GL, with a minimum in December at 20 m and a maximum in May at 45 m (Fig. 3). High salinity values throughout the water column were noted from December 2000 to March 2001, whereas salinity decreased slightly below 20 m from June to December 2001. Low salinity throughout the water column in GL (average 34.77) in December 2001 is consistent with data from previous years and could be caused by the flow of cold freshwater from the karstic spring 'Fontana' (Buljan & Špan 1976). Salinity in SL (Fig. 3) varied between 36.75 and 38.82 (yearly average = 38.31 ± 0.47). A pronounced halocline was found from January to May 2001, generally between 5 and 10 m, with the maximum gradient $\Delta S = 0.35$ m⁻¹ in March.

Oxygen saturation varied between 0.16 and 1.29 (0.94 ± 0.23 on average) in GL, and between 0.17 and 1.32 (0.93 ± 0.24 on average) in SL (Fig. 3). Surface

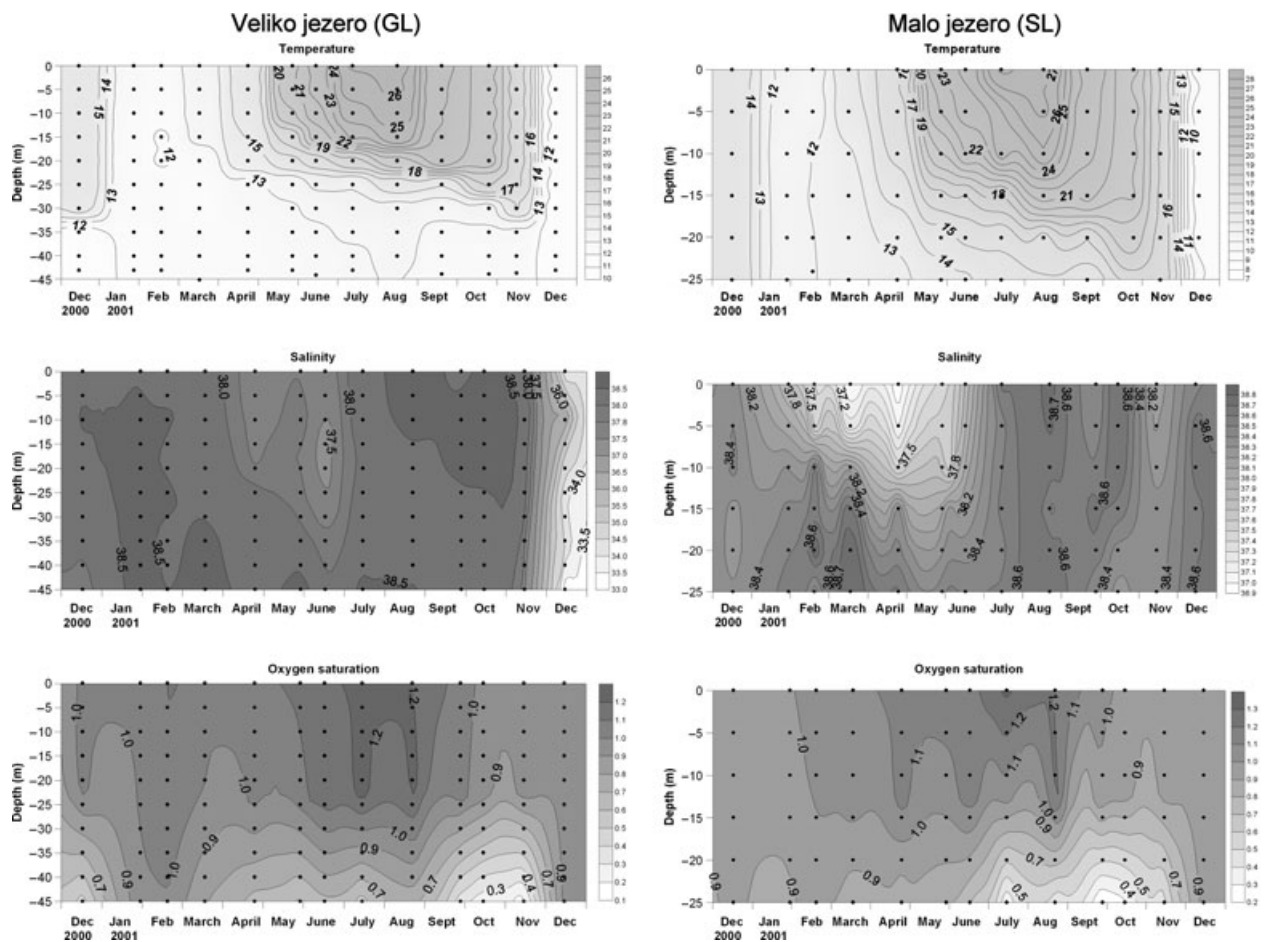


Fig. 3. Variation of temperature, salinity and oxygen saturation in the Veliko jezero great lake (GL) and Malo jezero small lake (SL) from December 2000 to December 2001.

Table 1. Temperature in Veliko jezero great lake (GL) and Malo jezero small lake (SL): surface, averages above and below the thermocline and average of the whole water column from December 2000 to December 2001.

	2000		2001																							
	December		January		February		March		April		May		June		July		August		September		October		November		December	
	GL	SL	GL	SL	GL	SL	GL	SL	GL	SL	GL	SL	GL	SL	GL	SL	GL	SL	GL	SL	GL	SL	GL	SL	GL	SL
Surface (°C)	15.5	14.5	12.6	11.9	12.2	11.3	13.6	14.0	15.3	15.5	20.6	23.0	22.5	24.3	26.2	28.3	26.4	27.6	22.1	22.7	20.8	20.7	17.2	16.7	11.5	9.1
AVG above TC (°C)	–	–	–	–	–	–	–	–	15.1	15.1	18.7	21.8	22.0	23.9	25.0	27.2	25.9	25.9	22.0	22.3	20.4	20.8	17.1	–	–	–
AVG below TC (°C)	–	–	–	–	–	–	–	–	12.5	12.8	12.7	14.5	13.2	15.6	13.3	15.4	13.9	14.6	13.3	14.7	12.8	16.6	12.6	–	–	–
Depth of TC (m)	–	–	–	–	–	–	–	–	20–25	15–20	20–25	10–15	15–20	10–15	15–20	10–15	15–20	10–15	20–25	15–20	25–30	15–20	30–35	–	–	–
WC AVG (°C)	14.2	14.6	12.3	11.6	12.1	11.8	12.7	13.1	13.8	14.3	15.7	18.2	17.0	19.4	18.4	19.1	19.9	22.1	17.5	19.8	17.3	19.4	15.7	16.7	11.5	9.1

VG, average; TC, thermocline; WC, water column.

AVG, average; TC, thermocline; WC, water column.

waters were generally well saturated throughout the year. Hypoxia occurred in near-bottom waters from September to November in both lakes.

Net zooplankton

Total net zooplankton abundance in Malo jezero (SL) was highest during the summer, with a maximum density in June and August of 14 072 and 14 118 ind. m⁻³, respectively. The lowest density of 1429 ind. m⁻³ was recorded in October. Copepods dominated, contributing 34–93% of total zooplankton abundance. Cyclopoids, with *Oithona nana* as the dominant species, contributed most to total copepod abundance (34–92%, Fig. 4). Calanoids, dominated by *Paracalanus parvus*, made up 10–68% of total copepods. Poecilostomatoids and harpacticoids made up less than 4 and 6%, respectively, of total copepod abundance (Fig. 4). Zooplankton other than copepods (ZOC), mainly bivalve larvae (>80% of the total ZOC), were abundant in July and August, with densities of 7767 and 7955 ind. m⁻³, respectively (Fig. 4). Appendicularians, chaetognaths and pteropods contributed 5–30% of total ZOC. *Muggiaea atlantica* made up less than 5% of total ZOC.

Maximum zooplankton abundance in Veliko jezero (GL) was recorded in April in the 0–20 m depth layer (12 215 ind. m⁻³) and in June at 20–40 m depth (11 617 ind. m⁻³). Copepods were the dominant group, contributing between 20 and 96% of total zooplankton abundance (Fig. 4). Cyclopoids and calanoids made up >90% of the total copepod catch (Fig. 4). The cyclopoid *O. nana* and the calanoid *P. parvus* were the dominant species in both the 0–20 m and 20–40 m layers. Poecilostomatoids and harpacticoids contributed less than 10% to total copepod abundance (Fig. 4). In GL, the maximum density of zooplankton other than copepods occurred in April in the 0–20 m layer (2269 ind. m⁻³), and in September in the 20–40 m layer (3971 ind. m⁻³). Pteropods and bivalve larvae contributed 69 and 98%, respectively, to total ZOC during the April and September maxima.

Calycophoran *Muggiaea atlantica*

Muggiaea atlantica occurred in Malo jezero (SL) throughout 2001, with higher abundances between May and August. Gonophores reached their greatest density (141 per m³) in May, followed by a peak of nectophores (37 per m³) in June (Fig. 5). Calyconula larvae were present in SL from May to September, with a maximum density (80 per m³) in June (Fig. 5).

In contrast to SL, in Veliko jezero (GL) *M. atlantica* occurred only between September and November 2001. Nectophores were mainly concentrated in the upper

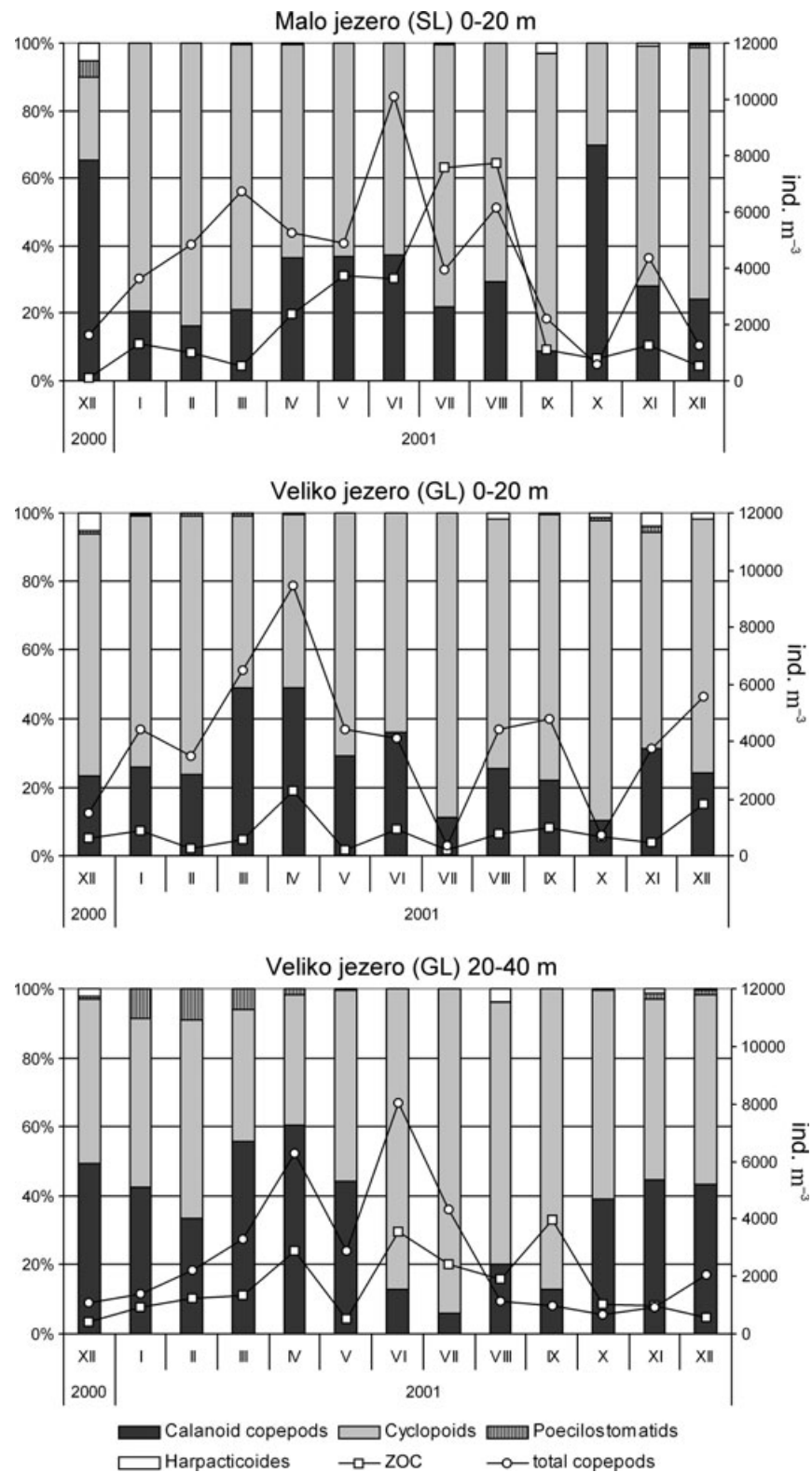


Fig. 4. Total copepod abundance (ind. m^{-3}) with the relative contribution of each group (%) and total abundance of other zooplankton, ZOC (ind. m^{-3}) in Malo jezero small lake (SL) and Veliko jezero great lake (GL) from December 2000 to December 2001.

20 m while gonophores were distributed across the whole water column (Fig. 5). A maximum of 0.64 nectophores and 10.24 gonophores per m^3 were recorded in October 2001 between 0 and 20 m depth. No calyconula larvae were found in GL.

Temperature and *M. atlantica* abundance co-varied in both GL and SL (PCA analyses, Fig. 6). In SL, high densities of *M. atlantica* nectophores and gonophores were recorded when the temperature below the thermocline and the oxygen concentration were relatively high and when copepods (in particular calanoids and cyclopoids) and bivalves were abundant (Fig. 6). In GL, *M. atlantica* was negatively correlated with chlorophyll *a*, O_2 concentration and with poecilostomatoid copepods (Fig. 6).

Discussion

Since 1995 *Muggiaea atlantica* has progressively established itself in the Southern Adriatic Sea, becoming an abundant calycophoran in coastal waters (Batistić 1999; Kršinić & Njire 2001; Lučić *et al.* 2005; Batistić *et al.* 2007). *Muggiaea atlantica* was found for the first time in the marine lakes of Mljet in 2001, at high abundance throughout the year in Malo jezero (SL). *Muggiaea kochi* was previously reported as the sole calycophoran in GL (Vučetić 1957, 1966, 1995; Lučić & Bender-Pojatina 1995) but during 2001 it was not found in the Mljet lakes.

The temporal sequence of occurrence of *M. atlantica* nectophores, gonophores and calyconula larvae suggests

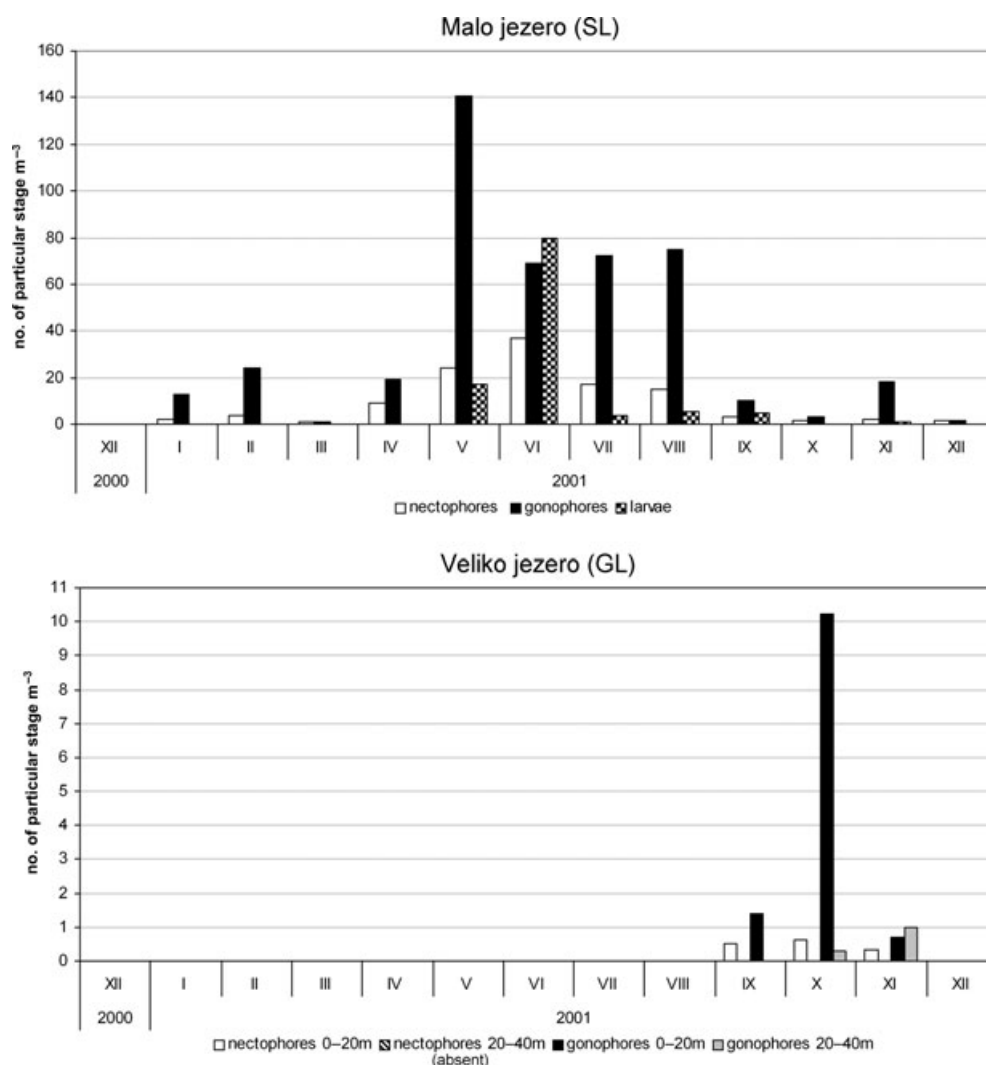


Fig. 5. Variation in the abundance of *Muggiaea atlantica* nectophores, gonophores and larvae (per m^3) in Malo jezero small lake (SL) and Veliko jezero great lake (GL) from December 2000 to December 2001.

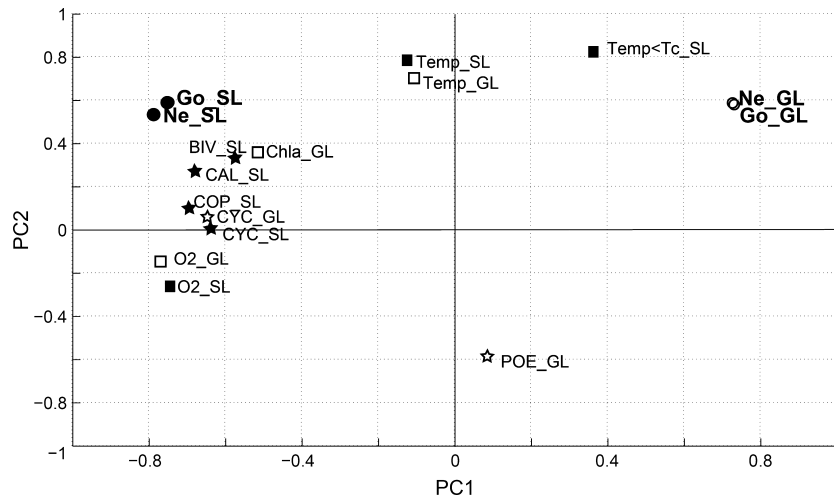


Fig. 6. Results of the principal component analysis (PCA) performed on the monthly abundance of *Muggiaea atlantica* nectophores and gonophores in Veliko jezero great lake (GL) and Malo jezero small lake (SL). The environmental (squares) and biological (stars) descriptors best correlated to the PC1 and PC2 are also shown. Empty symbols identify data from GL, while full symbols identify data from SL. Nc, nectophores; Go, gonophores; Chl a, integrated chlorophyll a; O2, integrated oxygen concentration; Temp, integrated temperature; Temp < Tc, temperature below the thermocline; BIV, bivalve larvae; CAL, calanoid copepods; COP, total copepods; CYC, cyclopoid copepods; POE, poecilostomatoid copepods.

that this species underwent a complete life cycle in SL, actively reproducing from May to September when the water column was well stratified. The PCA analysis indicated that high abundance of *M. atlantica* in SL was mainly related to higher temperatures, in particular values below the thermocline (average 14.5–15.6 °C). It seems that high temperatures above the thermocline (>24 °C) in SL during summer depress the presence of *M. atlantica* in this layer. Marques *et al.* (2008) found a steep decline in the abundance of *M. atlantica* in waters warmer than 24 °C. Records of *M. atlantica* nectophores and gonophores during the winter of 2001 indicate that this species was able to successfully generate sexual eudoxids in SL at temperatures <13 °C. However, calyconulae larvae did not appear before May. This suggests that gonophores matured more slowly at lower winter temperatures than in spring–summer. Higher temperatures in the spring–summer period trigger the fast release of eudoxids and maturation of gonophores, and as a consequence there is a rapid growth in abundance of the population of *M. atlantica*.

The PCA analysis also indicated that high abundance of *M. atlantica* in SL was related to high abundance of planktonic prey. According to Purcell (1982) the number of eudoxids produced by *M. atlantica* and their growth rate tend to increase with the density of prey, mainly nauplii and the juvenile stages of small copepods. The positive correlation between *M. atlantica* density in SL and the abundance of the small copepods, in particular the cyclopoid *Oithona nana* and the calanoid *Paracalanus*

parvus, seems to support this hypothesis. *Muggiaea atlantica*, known to be a voracious predator, needs an average of 2000 copepods per day to sustain a population of 100 colonies per m³ (Purcell 1982). The abundance of copepods (cyclopoids and calanoids) decreased in May, which is in accordance with high densities of *Muggiaea atlantica* nectophores and gonophores.

Muggiaea atlantica nectophores and gonophores were found in low numbers in GL, mainly in the upper 20 m, between September and November 2001. There were no larvae. This suggests that *M. atlantica* was not efficiently reproducing in GL and that its presence there likely was the result of transport through the shallow (2.5 m) and narrow Soline Channel. This transport is limited by this area's small tidal range, but the inflow from the open sea tends to increase during the warmer seasons (Buljan & Špan 1976). In addition, an upwelling recorded at the open sea near the Soline Channel at the end of the summer (Buljan & Špan 1976) brings species that usually occur below the thermocline to the surface; these species may then be advected into GL. Different factors could cause the low productivity of *M. atlantica* in GL. For example, temperatures below the thermocline in GL during the period of stratification were always lower than in SL (on average 2 °C). This is consistent with previous investigations that reported differences of up to 6 °C between the two lakes (Buljan & Špan 1976; Jasprica *et al.* 1995; Benović *et al.* 2000). Temperatures below the thermocline in GL, therefore, may have been too low to allow an efficient growth of the population of *M. atlantica*

during the warmer seasons. High temperatures above the thermocline in GL also may have been limiting. The swarms of the scyphomedusa *Aurelia* sp. regularly reported in GL suggest that *M. atlantica* was exposed to higher predation pressure than in SL, where *Aurelia* was only found occasionally (Benović *et al.* 2000; Malej *et al.* 2007; Turk *et al.* 2008; Alvarez Colombo *et al.* 2009).

According to Rutherford & Thuesen (2005), *M. atlantica* is an oxyconformer and shows good tolerance to hypoxic conditions. When it was most abundant in SL, the water column was well aerated both above and below the thermocline. Hypoxic conditions were observed only near the bottom, from September to November in both lakes.

It therefore seems reasonable to conclude that, of the two marine lakes, Malo jezero (SL) presented a more suitable habitat for *M. atlantica*, mainly because of favorable temperatures below the thermocline, more abundant prey and possibly lower predation pressure.

Previous investigations reported no calyophorans in SL and *M. kochi* as the only calyophoran in GL (Vučetić 1957, 1966; Lučić & Bender-Pojatina 1995). *Muggiaea kochi* typically was present throughout the year in GL, with higher numbers in August and September (Vučetić 1961, 1966). This species, which is a neritic warm-water species with a preference for relatively high temperatures (Alvariño 1974), was concentrated mainly in the upper 20 m (above the thermocline) in summer (Vučetić 1961). A complete life cycle of *M. kochi*, including release of eudoxids by the polygastric colony, has been described for temperatures between 18 and 24 °C, while at a temperature of 13 °C only the polygastric phase (nectophores) was observed (Carré & Carré 1991). We therefore hypothesize that the winter temperatures below 13 °C recorded in GL during 2000/2001 limited the occurrence of *M. kochi* there. Some nectophores of *M. kochi* still may have survived below 13 °C, but without production of eudoxids it would have been impossible to start a new generation the following spring. Therefore, the autochthonous *M. kochi* might not have been competitively displaced by the allochthonous *M. atlantica*. This is also supported by the preference of *M. atlantica* for SL, contrary to *M. kochi*. Further, in general, during the warmest period, *M. kochi* (Vučetić 1961) and *M. atlantica* seek different temperature niches (i.e. above and below the thermocline, respectively). According to the above hypothesis, the occurrence of *M. kochi* in GL depends on constant repopulation from the open sea.

Based on earlier reports, these two congeneric species rarely occur in the same ecosystem (Russell 1934; Alvariño 1974; Mackie *et al.* 1987). After 1980, however, they did co-exist in the Ligurian Sea (Licandro & Ibanez 2000), and after 1995 in the Adriatic Sea (Batistić *et al.* 2007). Suitable hydrographic conditions and the stronger

inflow of less saline, colder Atlantic water (Civitaresse *et al.* 2010) likely enabled the immigration of *M. atlantica* from the Western Mediterranean to the Adriatic Sea. During 1996, *M. kochi*, the most numerous Adriatic calyophore (Gamulin & Kršinić 1993), decreased in abundance, whereas *M. atlantica* constituted more than 30% of total calyophoran nectophores during winter and late summer (Batistić *et al.* 2007). It thus seems that the occurrence of these two congeners is driven by hydroclimatic changes, in particular the temperature regime, as temperature is the key determinant of their reproductive success. In view of ongoing climatic changes, it seems paradoxical that cold-temperate species such as *M. atlantica* would expand their geographical range within an already subtropical sea such as the Mediterranean. The arrival of *M. atlantica* into the Adriatic was caused by circulation shifts, which in turn depend on larger scale processes. This is a likely scenario for future colonisations in which alien species arrive due to climate-induced disruption of circulation barriers.

Overall, the results of this study demonstrate that *M. atlantica* has the potential to increase in abundance very rapidly when environmental conditions are favourable. It has, indeed, adapted to the shallow closed ecosystem of the Mljet lakes more successfully than its congener *M. kochi* has.

Acknowledgements

We wish to thank anonymous referees and the Editors for constructive criticism and valuable comments. Many thanks also to Mr Steve Latham (Dubrovnik, Croatia) and Mr Mike Blackett (Plymouth, UK) for improving the language of the manuscript. This work was supported by the Croatian Ministry of Science, Education, and Sports (Grant Numbers 275-0000000-3186 and 275-0982705-3047). The publication of this paper is supported by CONISMA, the Italian National Interuniversity Consortium for Marine Sciences.

Conflicts of Interest

None of the authors have any potential conflicts of interest.

References

- Alvarez Colombo G., Benović A., Malej A., Lučić D., Makovec T., Onofri V., Acha M., Madirolas A., Mianzan H. (2009) Acoustic survey of a jellyfish-dominated ecosystem (Mljet Island, Croatia). *Hydrobiologia*, **616**, 99–111.
- Alvariño A. (1974) Distribution of siphonophores in the regions adjacent to the Suez and Panama Canals. *Fishery Bulletin*, **72**, 527–546.

- Batistić M. (1999) *Macrozooplankton in the South Adriatic Pit*. Ph.D. Thesis, University of Zagreb, Zagreb.
- Batistić M., Jasprica N., Carić M., Lučić D. (2007) Annual cycle of the gelatinous invertebrate zooplankton of the eastern South Adriatic coast (NE Mediterranean). *Journal of Plankton Research*, **29**, 671–686.
- Benović A., Lučić D., Onofri V., Peharda M., Carić M., Jasprica N., Bobanović-Čolić S. (2000) Ecological characteristics of the Mljet Island seawater lakes (South Adriatic Sea) with special reference to their resident populations of medusae. *Scientia Marina*, **64**, 197–206.
- Bouillon J., Medel M.D., Pagès F., Gili J.M., Boero F., Gravili C. (2004) Fauna of the Mediterranean Hydrozoa. *Scientia Marina*, **68**(Suppl. 2), 5–438.
- Buljan M., Špan J. (1976) Hydrographical properties of the sea water 'Lakes' on the island of Mljet and adjoining sea in the eastern south Adriatic Sea. *Acta Adriatica*, **6**, 1–224.
- Carré C., Carré D. (1991) A complete life cycle of the calyphoran siphonophore *Muggiaea kochi* (Will) in the laboratory, under different temperature conditions: ecological implications. *Philosophical Transactions: Biological Sciences*, **334**, 27–32.
- Civitaresi G., Gačić M., Lipizer M., Borzelli G.L.E. (2010) On the impact of the Bimodal Oscillating System (BIOS) on the biogeochemistry and biology of the Adriatic and Ionian Seas (Eastern Mediterranean). *Biogeosciences Discussions*, **7**, 6971–6995.
- Gamulin T., Kršinić F. (1993) Distribution and abundance of calyphores (Siphonophora, Calyphorae) in the Mediterranean and Adriatic Sea. *Marine Ecology*, **14**, 97–111.
- Gamulin T., Kršinić F. (2000) Calyphores (Siphonophora, Calyphorae) of the Adriatic and Mediterranean Seas. *Natura Croatica*, **9**, 1–198.
- Gili J.M., Pagès F., Sabatés A., Ros J.D. (1988) Small-scale distribution of a cnidarian population in the western Mediterranean. *Journal of Plankton Research*, **10**, 385–401.
- Grasshoff K. (1983) Determination of salinity. In: Grasshoff K., Ehrhardt M., Kremling K. (Eds), *Methods of seawater analysis. Second, revised and extended edition*. Verlag Chemie, New York: 419.
- Ianora A., Scotto di Carlo B. (1981) The distribution and annual cycles of Siphonophora Calyphora in the Gulf of Naples and adjacent waters. *Archivio di Oceanografia e Limnologia*, **20**, 51–65.
- Jasprica N., Viličić D., Carić M., Njire J. (1995) Fitoplankton u Malom i Velikom jezeru (otok Mljet, južni Jadran). In: Durbešić P., Benović A. (Eds), *Simpozij 'Prirodne značajke i društvena valorizacija otoka Mljeta'*, Pomena. Hrvatsko ekološko društvo, Zagreb: 453–463.
- Kršinić F., Njire J. (2001) An invasion by *Muggiaea atlantica* Cunningham 1892 in the northern Adriatic Sea in the summer of 1997 and the fate of small copepods. *Acta adriatica*, **42**, 49–59.
- Licandro P., Ibanez F. (2000) Changes of zooplankton communities in the Gulf of Tigullio (Ligurian Sea, Western Mediterranean) from 1985 to 1995. Influence of hydroclimatic factors. *Journal of Plankton Research*, **22**, 2225–2253.
- Licandro P., Souissi S., Ibanez F., Carré C. (2012) Long-term variability and environmental preferences of calyphoran siphonophores in the Bay of Villefranche (north-western Mediterranean). *Progress in Oceanography*, **97–100**, 152–163.
- Lučić D., Bender-Pojatina A. (1995) Net zooplankton of Mljet lakes. In: Durbešić P., Benović A. (Eds), *Simpozij 'Prirodne značajke i društvena valorizacija otoka Mljeta'*, Pomena. Hrvatsko Ekološko društvo, Zagreb: 483–498.
- Lučić D., Benović A., Batistić M., Njire J., Onofri V. (2005) Calyphorae (Siphonophora) in the open waters of the central and south Adriatic Sea during spring 2002. *Journal of the Marine Biological Association of the United Kingdom*, **85**, 495–501.
- Mackie G.O., Pugh P.R., Purcell J.E. (1987) Siphonophore biology. *Advances in Marine Biology*, **24**, 97–262.
- Malej A., Turk V., Lučić D., Benović A. (2007) Direct and indirect trophic interactions of *Aurelia* sp. (Scyphozoa) in a stratified marine environment (Mljet Lakes, Adriatic Sea). *Marine Biology*, **151**, 827–841.
- Marques S.C., Azeiteiro U.M., Leandro S.M., Queiroga H., Primo A.L., Martinho F., Viegas I., Pardal M.A. (2008) Predicting zooplankton response to environmental changes in a temperate estuarine ecosystem. *Marine Biology*, **155**, 531–541.
- Moser F. (1925) Die Siphonophoren der Deutschen Südpolar-Expedition 1901-1903. In: von Drygalski E. (Ed.), *Deutschen Südpolar-Expedition*. Berlin: Walter de Gruyter & Co.: 1-604.
- Purcell E.J. (1982) Feeding and growth of the siphonophore *Muggiaea atlantica* (Cunningham 1893). *Journal of Experimental Marine Biology and Ecology*, **62**, 39–54.
- Russell F.S. (1934) On the occurrence of the siphonophores *Muggiaea atlantica* Cunningham and *Muggiaea kochi* (Will) in the English Channel. *Journal of the Marine Biological Association of the United Kingdom*, **19**, 555–558.
- Russell F.S. (1938) On the development of the *Muggiaea atlantica* Cunningham. *Journal of the Marine Biological Association of the United Kingdom*, **22**, 441–446.
- Rutherford L.D., Thuesen E.V. (2005) Metabolic performance and survival of medusae in estuarine hypoxia. *Marine Ecology Progress Series*, **294**, 189–200.
- Schmidt R. (1993) Environmental changes in two Adriatic coastal lakes in the time interval 7,500–5,000 B.P. (Atlantic) with special reference to the diatom succession of *Cyclotella*. *Limnologia*, **23**, 47–58.
- Strickland J.D.H., Parsons T.R. (1972) *A Practical Handbook of Seawater Analysis*, 2nd edn. Bulletin 167. Fisheries Research Board of Canada, Ottawa: 310 pp.
- Turk V., Lučić D., Flander-Putrlje V., Malej A. (2008) Feeding of *Aurelia* sp. (Scyphozoa) and links to the microbial food web. *Marine Ecology*, **29**, 495–505.

- UNESCO (1973) *International Oceanographic Tables*, Vol. II UNESCO, Paris: 141.
- Vilibić I., Žuljević A., Nikolić V. (2010) The dynamics of a saltwater marine lake (Big Lake, Island of Mljet, Adriatic Sea) as revealed by temperature measurements. *Acta Adriatica*, **51**, 119–130.
- Vučetić T. (1957) Zooplankton investigations in the sea water lakes Malo jezero and Veliko jezero on the island of Mljet (1952–1953). *Acta Adriatica*, **6**, 1–47.
- Vučetić T. (1961) Quelques données préliminaires sur la répartition verticale du zooplancton dans la baie Veliko Jezero de l'île de Mljet pendant l'été. *Rapports et Procès-verbaux des Réunions – Commission Internationale pour l'exploration scientifique de la mer Méditerranéen*, **16**, 149–151.
- Vučetić T. (1966) Quantitative ecology investigations of the zooplankton during the fertilization experiments in the Bay Veliko jezero (I. Mljet). *Acta Adriatica*, **6**, 1–28.
- Vučetić T. (1995) Oceanographic investigations of the Small and the Big Lake on the Island Mljet – historical review. In: Durbešić P., Benović A. (Eds), *Simpozij 'Prirodne značajke i društvena valorizacija otoka Mljeta'*, Pomena. Hrvatsko Ekološko društvo, Zagreb: 401–413.
- Weiss R.F. (1970) The solubility of nitrogen, oxygen and argon in water and seawater. *Deep-Sea Research*, **17**, 721–735.
- Zore-Armanda M., Bone M., Dadić V., Morović M., Ratković D., Stojanovski L., Vukadin I. (1991) Hydrographic properties of the Adriatic Sea. *Acta Adriatica*, **32**, 5–540.