Benthic Foraminiferal Assemblages in a Restricted Environment - An Example from the Mljet Lakes (Adriatic Sea, Croatia)

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Key words: Benthic foraminifera, Anoxia, Restricted environment, Elphidium, Haynesina, Mljet Island, Adriatic Sea, Croatia.

Abstract

Benthic foraminiferal assemblages from a peculiar restricted marine environment, the Mljet Lakes (Mljet Island, Adriatic Sea, Croatia) have been studied. These lakes are drowned karst dolines, which are connected with the Adriatic Sea through a narrow, shallow channel. Occasional stagnant conditions in the marine lakes cause hypoxic and anoxic conditions in the bottom waters. Such stressed conditions are reflected in oligospecific benthic foraminiferal assemblages with a Shannon-Wiener species diversity index (H) ranging from 0.8 to 1.0 and equitability index (E) ranging from 0.18 to 0.26, identified in samples from each marine lake. In the more dysoxic Malo Jezero, Haynesina depressula dominates an assemblage of 12 benthic foraminiferal species. In the less (and less frequently) hypoxic Veliko Jezero, we found an Asterigerinata mamilla assemblage with 18 foraminiferal species. A more diverse assemblage containing 55 different benthic foraminiferal species occupies an adjacent open-sea station.

Long-term salinity measurements indicate that H. depressula tolerates higher salinity than formerly presumed (up to 38 ppt), and is well adapted to stressed hypoxic conditions.

1. INTRODUCTION

Veliko and Malo Jezero (the Mljet Lakes) are natural phenomena on Mljet Island (Adriatic Sea). Due to its scenic beauty, ecological and environmental values the western part of the island was proclaimed a National Park in 1960 (Fig. 1). Veliko and Malo Jezero (Large and Small Lake = Mljet Lakes) are semi-enclosed depressions connected with the open sea by a narrow, shallow channel. The lakes are typical karst depressions (dolines or sinkholes), which were formed under subaerial exposure and are now submerged due to Holocene sea-level rise. Being connected with the sea, they have saline marine water and therefore are not true lakes, but can be termed marine lakes. Morphometric characteristics of the Mljet Lakes were reported in VULETIĆ (1953), along with their geological setting and sediment characteristics.

Weak tidal currents and feeble wind influence cause expressed stratification of the water column, giving rise to temporary stagnant conditions in the marine lakes, especially in Malo Jezero (BULJAN & ŠPAN, 1976; BENOVİĆ et al., 2000). Therefore the Mljet Lakes are restricted environments not only in a spatial sense, but also in the sense of stress-producing factors (SEIBOLD & BERGER, 1996).

The aim of this preliminary research was to compare benthic foraminiferal assemblages, including foraminiferal morphological variations, with hydrological, sedimentological, and ecological characteristics of such a peculiar, restricted, unstable environment in the karstified marine depressions. In spite of the worldwide distribution of karstic phenomena, there are very few papers dealing with the various organisms inhabiting such areas (CIMERMAN et al., 1988; SOKAČ & BAJRAKTAREVIĆ, 1995).

CIMERMAN et al. (1988) found two different foraminiferal assemblages in Veliko Jezero. In coarse-grained sediment at 30 m depth miliolids occurred in large number, while in the muddy bottom (at 42 m depth) agglutinated foraminifera were dominant, implying low temperature, low oxygen content and reduced light (ibid, p. 745). In contrast, SOKAČ & BAJRAKTAREVIĆ (1995, p. 130) have described in the same marine lake, but at 8 m depth in the >250 µm size fraction a typical shallow-marine foraminiferal assemblage with a prevalence of porcellaneous and agglutinated species. In a sample from 30 m depth they found that hyaline foraminifera dominate the assemblage.

Salinity data in this paper are reported simply as numbers, because the salinity has been defined since the early 1980’s as the ratio between conductivity of seawater and of standard KCl solution (OPEN UNIVERSITY COURSE TEAM, 1989).

2. STUDY AREA

2.1. HYDROGRAPHY

Water exchange between the open sea and Veliko Jezero and Malo Jezero is driven by tidal currents. However, the average tidal amplitude in this area is only 11 ± 0.5 cm (BULJAN & ZORE-ARMANDA, 1976). The Veliki Most (Large Bridge) strait between
the Soline Channel and Veliko Jezero is only 10 m wide and 2.5 m deep. Prior to artificial enlargement in 1960 it was only 4.5 m wide and 0.6 m deep (STRAŽIĆ, 1979). The Mali Most (Small Bridge) strait between Veliko and Malo Jezero is even smaller: 2.5 m wide and 0.2 m deep. Therefore the masses of water exchanged are small. Mean annual precipitation (1981-1990) at the nearby meteorological station Govedari is 765 mm, and potential evapotranspiration is 692.6 mm/year, indicating the slightly humid climatic characteristics of the region. However, precipitation is concentrated in winter, whereas during summer evaporation prevails (VUÈETIÆ & VUÈETIÆ, 1995). Therefore, during the warm part of the year, due to excessive heating of the surface layer, large differences in density between surface and bottom waters occur. Dense bottom water formed in winter cannot be exchanged during summer. The concentration of organic matter increases in summer, and this causes enhanced bacterial degradation and oxygen undersaturation in the deepest parts of the Mljet Lakes (CARIĆ & JASPRICA, 1995).

The summarized hydrographic data (Table 1, after BULJAN & ŠPAN, 1976; BENOVIĆ et al., 2000) indicate high salinity (36-38 ‰), relatively cold water (9-18°C), and episodic anoxic conditions in bottom water in both depressions (in Malo Jezero and in Veliko Jezero). For example, BULJAN & ŠPAN (1976) report that in 1951 to 1953 there was a permanent anoxia in the bottom waters in the Malo Jezero. BENOVIĆ et al. (2000) found that dissolved oxygen saturation near the bottom in October 1997 was 4.3% in Malo Jezero and 17% in Veliko Jezero. Moreover, they registered an anoxic event in the Veliko Jezero between August 26-28, 1996, when below the thermocline layer (at 18.5 m) oxygen concentration rapidly decreased to 0% in the layer from 39 m to the bottom. Open marine hydrographic conditions were found at the Križ station (Figs. 1, 2).

Due to vertical differences in temperature and salinity, the formation and depth of the seasonal thermocline differs at the locations investigated. In the open waters of Mljet Island (Križ station), the seasonal thermocline depth ranges between 11 and 42 m and its average depth is at 25 m. In Veliko Jezero, the thermocline is shallower (12-22 m) and shows little vertical change. In Malo Jezero, the thermocline is the shallowest (5-12
m), but also the most stable and the strongest, because of large temperature differences (Fig. 2). Occasionally, the thermocline formed during summer in Malo Jezero remains stable even during winter, thus preventing bottom water mixing for a period longer than a year (BULJAN & ŠPAN, 1976).

2.2. SEDIMENTS

Previous sedimentological research in the Mljet Lakes (VULETIĆ, 1953; SEIBOLD, 1958; CIMERMAN et al., 1988; JURAČIĆ et al., 1995) indicated similar sediment distribution in both lakes. The deepest part of Malo Jezero is covered with muddy sediment, whereas the bottoms above 17 m contain mainly zoogenous sand. A change in sediment type with depth can also be observed in Veliko Jezero, but it is not as regular as in Malo Jezero. The shallower parts of Veliko Jezero are covered with biogenous carbonate sands, whereas in the deeper parts (42 m) clay minerals and authigenic pyrite are present.

In sediment cores taken from both Malo Jezero and Veliko Jezero, microlamination is common. The laminae have been interpreted either as annual layers (varves) as a consequence of seasonal anoxic conditions (SEIBOLD, 1958; SEIBOLD & BERGER, 1996), or

<table>
<thead>
<tr>
<th>STATIONS</th>
<th>1. Malo Jezero (28 m)</th>
<th>2. Malo More (13 m)</th>
<th>3. Veliko Jezero (40 m)</th>
<th>4. Soline Channel (1.5 m)</th>
<th>5. Križ (Open Sea) (38 m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>salinity</td>
<td>36-38</td>
<td>34-36</td>
<td>35.5-37</td>
<td>36-38</td>
<td>38</td>
</tr>
<tr>
<td>temperature</td>
<td>9-18°C</td>
<td>9-28°C</td>
<td>9-17°C</td>
<td>9-27°C</td>
<td>13-16°C</td>
</tr>
<tr>
<td>oxygen concentration</td>
<td>0.0-6.6 ml/l</td>
<td>4.8-6.4 ml/l</td>
<td>0.0-6.6 ml/l</td>
<td>5-6 ml/l</td>
<td>4.2-6.6 ml/l</td>
</tr>
</tbody>
</table>

Table 1 Ranges of bottom water characteristics at investigated stations. Summarized data after BULJAN & ŠPAN (1976) and BENOVIC et al. (2000).
lamination due to episodic bottom-water anoxic events which need not necessarily correspond to annual variations (JURAJČIĆ et al., 1995).

3. SAMPLING AND METHODS

3.1. SAMPLING AND SAMPLE PREPARATION

Scuba divers collected sediment cores up to 80 cm long from five stations in the Mljet Lakes and the adjacent open sea (Fig. 1) in May 1995. Sediment cores were frozen within 4 hours, and transported frozen to the laboratory.

In the laboratory, frozen cores were cut into subsamples, and the first 2-cm subsamples were used for our research. After defrosting, a subsample of 10 ml of wet sediment was taken for foraminiferal analysis, and the rest of the subsample was used for grain-size analysis.

3.2. METHODS

The grain size of the sediment samples was analyzed by wet sieving, using ASTM standard stainless steel sieves for >32 µm fraction. A Coulter Counter (mod. TA II) was used for the <32 µm sizes. The sediments were classified according to their gravel - sand - mud (mud = silt + clay) ratio (FOLK, 1954).

Carbonate content was determined volumetrically by measuring CO₂ evolved by dissolving a 0.5 g dry sample in 15% HCl.

The subsamples for foraminiferal analysis were stained with rose Bengal (MURRAY, 1973), in spite of the disadvantages and limitations of this method (MURRAY, 1991; JORRISEN et al., 1995). After staining, subsamples were wet sieved through 250 and 125 µm sieves.

In each sample foraminifera were identified after FORAMINIFERI PADANI (1982), JORRISEN (1988), LOEBLICH & TAPPAN (1987), and CIMERMAN & LANGER (1991), and all specimens (stained and unstained) were counted. The absolute abundance in 10 ml, and the relative abundance of each species was determined. For each station, dominant and accessory species were defined according to their relative abundance. An estimation of the species diversity was performed using the following parameters: number of species, number of specimens, Shannon-Wiener species diversity index (H), equitability index (E) (BUZAS, 1979), and percentage of Miliolina (=porcellaneous), Textulariina (=agglutinated) and Rotaliina s.l. (=hyaline). Species diversity and abundance were compared with the known ecological conditions (temperature, salinity, substrate). The morphotype variations were described from >125 µm size-group foraminifera. Existing corollary hydrographic data gave a better understanding about the ecological affinity of investigated species. Sedimentation rate was estimated according to the relative abundance of specimens of sessile species (POAG et al., 1980).

4. RESULTS

4.1. GRANULOMETRIC ANALYSES

Results of granulometric analyses (mean size, sorting, mud percent, and sediment type), along with carbonate content of investigated samples, are reported in Table 2.

The sample from the deepest part of Malo Jezero (sample #1; 28 m depth) has only 4.9% biogenous particles/fragments of gravel and sand size, and the rest is silt and clay. The surface sediment is 71% carbonates, mostly aragonite, with lesser amounts of calcite, magnesian calcite, and dolomite. The remaining part is quartz and feldspar (SONDI et al., 1995). In the shallow part of Malo More (sample #2; 13 m depth), the

<table>
<thead>
<tr>
<th>SAMPLE</th>
<th>WATER DEPTH (m)</th>
<th>MEAN SIZE, Mz (µm)</th>
<th>SORTING So</th>
<th>MUD (%)</th>
<th>SEDIMENT TYPE (Folk, 1954)</th>
<th>CARBONATE (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Malo Jezero</td>
<td>28</td>
<td>10.9</td>
<td>1.61</td>
<td>95.1</td>
<td>slightly gravelly mud</td>
<td>72</td>
</tr>
<tr>
<td>2. Malo More</td>
<td>13</td>
<td>176.8</td>
<td>2.81</td>
<td>48.4</td>
<td>slightly gravelly sandy mud</td>
<td>89</td>
</tr>
<tr>
<td>3. Veliko Jezero</td>
<td>40</td>
<td>59.5</td>
<td>3.45</td>
<td>73.3</td>
<td>gravelly mud</td>
<td>62</td>
</tr>
<tr>
<td>4. Soline Channel</td>
<td>1.5</td>
<td>692.6</td>
<td>1.44</td>
<td>5.1</td>
<td>gravelly sand</td>
<td>76</td>
</tr>
<tr>
<td>5. Križ (Open Sea)</td>
<td>38</td>
<td>1659.8</td>
<td>2.02</td>
<td>12.2</td>
<td>gravelly muddy sand</td>
<td>59</td>
</tr>
</tbody>
</table>

Table 2 Granulometric properties, types of sediments, and carbonate content. Surface sediment sample (0-2 cm), Mljet, May 1995.
sediment has 51.5% biogenous gravel and sand; the remainder is mud. Sample #3 (40 m depth) in Veliko Jezero contains 26.5% biogenous particles (>125 µm). The bottom of the shallowest part of the Soline Channel (sample #4; 1.5 m depth) contains carbonate gravelly sand, which forms symmetrical ripples. Their wave lengths are 3-6 m, as a consequence of the relatively strong tidal currents in that shallow channel. Sediment sorting is therefore better than in other samples (although still low =1.44). The nearshore marine sample #5 (Križ, 38 m depth) had the largest mean size (1660 µm), with 21.42% gravel, 66.43% sand, and the minimum carbonate.

4.2. DIVERSITY OF SPECIES AND ASSEMBLAGES, MORPHOTYPE VARIATIONS, AND SEDIMENTATION RATE

The numbers of stained, unstained, and total specimens, along with the number of species present in each sample, are reported in Table 3. In total, 67 benthic foraminiferal species were determined, and 44 species were represented by stained specimens in at least one sample (Table 4). The ratio between unstained and stained specimens (U/S) varies from 10:1 (#1 and 2) to 4:1 (#4) (Table 3). Six species were found only in the marine lakes, and 10 were restricted to the open water.

The open sea Križ sample (Station #5; 38 m depth) was the only one in which Textulariina exceeded 1%. The Rosalina bradyi - Cibicides refugens Assemblage contained 55 species with 876 specimens (H = 1.48, E = 0.26) (Tables 3, 5, 6). Biogenous fragments form an ideal substrate for such sessile species. Beside R. bradyi and C. refugens, the sample contained G. lobatulus, A.

Table 3 Number of species, unstained and stained individuals and total number of specimens in each sample, Mljet, May 1995.

<table>
<thead>
<tr>
<th>SAMPLE</th>
<th>DRY WEIGHT IN 10 ml (g)</th>
<th>SPECIMENS IN GRAM OF SEDIMENT</th>
<th>SPECIES</th>
<th>UNSTAINED SPECIMENS (U)</th>
<th>STAINED SPECIMENS (S)</th>
<th>Ratio U/S</th>
<th>TOTAL SPECIMENS</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Malo Jezero</td>
<td>8.29</td>
<td>15.9</td>
<td>12</td>
<td>120</td>
<td>12</td>
<td>10:1</td>
<td>132</td>
</tr>
<tr>
<td>2. Malo More</td>
<td>9.59</td>
<td>102.0</td>
<td>32</td>
<td>887</td>
<td>91</td>
<td>10:1</td>
<td>978</td>
</tr>
<tr>
<td>3. Veliko Jezero</td>
<td>6.29</td>
<td>23.2</td>
<td>18</td>
<td>122</td>
<td>24</td>
<td>5:1</td>
<td>146</td>
</tr>
<tr>
<td>4. Soline Channel</td>
<td>9.23</td>
<td>196.1</td>
<td>38</td>
<td>1462</td>
<td>348</td>
<td>4:1</td>
<td>1810</td>
</tr>
<tr>
<td>5. Križ (Open Sea)</td>
<td>10.02</td>
<td>87.4</td>
<td>55</td>
<td>771</td>
<td>105</td>
<td>7:1</td>
<td>876</td>
</tr>
</tbody>
</table>
## STATIONS

<table>
<thead>
<tr>
<th>FORAMINIFERA</th>
<th>1. MALO</th>
<th>2. MALO</th>
<th>3. VELIKO</th>
<th>4. SOLUNE</th>
<th>5. KRIŽ</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>JEZERO</td>
<td>MORE</td>
<td>JEZERO</td>
<td>CHANNEL</td>
<td>(OPEN SEA)</td>
</tr>
<tr>
<td></td>
<td>unstained</td>
<td>stained</td>
<td>unstained</td>
<td>stained</td>
<td>unstained</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>120</td>
<td>100</td>
<td>887</td>
<td>100</td>
<td>91</td>
</tr>
</tbody>
</table>

### TEXTULARIINA

- **Textularia sp.**
  - No.: 1
  - %: 0.11
  - No.: 1
  - %: 0.9

### MILIOLINA

- **Vertebrina striata**
  - No.: 21
  - %: 2.4
  - No.: 1
  - %: 1.1

- **Adelosina mediterranea**
  - No.: 3
  - %: 0.3

- **Spiriloculina ornata**
  - No.: 9
  - %: 1.0

- **Siphonaperta aspera**
  - No.: 72
  - %: 4.9

- **Cycloforina contorta**
  - No.: 3
  - %: 0.2

- **C. juleana**
  - No.: 10
  - %: 0.7

- **C. villafranca**
  - No.: 3
  - %: 0.4

- **C. colomi**
  - No.: 1
  - %: 0.1

- **Lachlanella variolata**
  - No.: 1
  - %: 0.1

- **Massilia secans**
  - No.: 1
  - %: 0.1

- **M. gualtieriana**
  - No.: 1
  - %: 0.1

- **Quinqueloculina nodulosa**
  - No.: 2
  - %: 0.3

- **Q. laevigata**
  - No.: 18
  - %: 15

- **Q. limbata**
  - No.: 3
  - %: 4

- **Textularia sp.**
  - No.: 1
  - %: 0.1

- **Textularia sp.**
  - No.: 10
  - %: 0.7

- **T. schreiberiana**
  - No.: 1
  - %: 0.1

- **Pyrgo sp.**
  - No.: 2
  - %: 0.2

- **Sigmoilinita costata**
  - No.: 1
  - %: 0.1

- **Wellmanelinella striata**
  - No.: 3
  - %: 2.5

- **M. webbiana**
  - No.: 1

- **Pseudotriloculina laevigata**
  - No.: 1

- **P. oblonga**
  - No.: 4

- **T. marioni**
  - No.: 1

- **T. schreiberiana**
  - No.: 1

- **T. webbiana**
  - No.: 1

- **T. semicostata**
  - No.: 2

- **M. gualtieriana**
  - No.: 1

- **Quinqueloculina nodulosa**
  - No.: 4

- **Q. laevigata**
  - No.: 15

- **Q. limbata**
  - No.: 3

- **Asterigerinata mamilla**
  - No.: 3

- **Gavelinopsis lobatulus**
  - No.: 3

- **Rosalina bradyi**
  - No.: 1

- **R. macropora**
  - No.: 3

- **Haynesina depressa**
  - No.: 39

- **V. bradyana**
  - No.: 20

- **Eponides concameratus**
  - No.: 1

- **Neoconorbina terquemi**
  - No.: 48

- **Asterigerinata mamilla**
  - No.: 3

- **Ammonia parkinsoniana**
  - No.: 6

- **A. tepida**
  - No.: 18

- **Lagen sp.**
  - No.: 2

- **Buccella sp. 1**
  - No.: 8
mamilla, *E. crispum* and in much smaller amount spine specimens of *E. aculeatum*. Several different species of Miliolina were also present (Table 4).

Morphotype variations were only found in the *Elphidium crispum* species (Fig. 2). Two morphotypes have been distinguished based on the following features (after JORRISEN, 1988): (1) maximum diameter; (2) number of chambers per final whorl; (3) structure and ornamentation of the umbilical part of the tests (the presence or absence of defined umbilical boss); (4) degree of inflation of the chambers (their shape); (5) outline of the test. Morphotype #1 of *E. crispum* species is a thin-shelled, flattened form with the maximum size reaching 1.44 mm, with a high number of arcuate chambers (27–29) in the last whorl, and with 12–14 ponticuli with subelliptical fossettes in last chamber. The sutures are backward curved, with a pronounced umbilical knob with 7–9 large perforations, and with angular peripheral margin.

Morphotype #2 is characterized by thick-shelled, lenticular, inflated tests, the maximum size is up to 0.57 mm; low number of arcuate chambers (10–14) in the last whorl, 9–12 ponticuli in the last chamber, the fossettes between ponticuli are rectangular in shape, chambers gradually increasing in size. The sutures are backward curved, with a flat umbilical knob.

In Malo More and Veliko Jezero (samples #2 and #3 respectively), morphotype #1 prevails (in sample #2 morphotype #1 makes 90% of all elphidiids found at this station, and in sample #3 it participates with 67%). In sediment samples from the Soline Channel and Križ (#4 and 5), morphotype #2 strongly prevails (87% and 91% respectively) (Fig. 2).

Along with the distribution of morphotypes of *E. crispum*, the occurrence of *E. aculeatum* is shown in Fig. 2. It was found only in samples from Stations #4, and #5. Bottom sediment type at investigated locations is also presented in Fig. 2.

The percentage of specimens of attached species *Cibicides*, *Rosalina* and *Planorbulina* differs significantly from station to station (Fig. 3). In Malo Jezero, specimens of these species were not recorded, but toward the open sea their percentage significantly increases, up to 11.7% in the unstained assemblage and 14.7% in the stained assemblage at the station Križ. The percentage of sessile specimens in the stained

<table>
<thead>
<tr>
<th>STATIONS</th>
<th>UNSMANID ASSEMBLAGES</th>
<th>STAINED ASSEMBLAGES</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>dominant species</td>
<td>secondary species</td>
</tr>
<tr>
<td>1. Malo Jezero</td>
<td>Haynesina depressula</td>
<td>Valvulinera bradyana, Ammonia tepida, Quinqueloculina laevigata</td>
</tr>
<tr>
<td>2. Malo More</td>
<td>Peneroplis planatus</td>
<td>Peneroplis pertusus, Asterigerinata mamilla</td>
</tr>
<tr>
<td>3. Veliko Jezero</td>
<td>Asterigerinata mamilla</td>
<td>Valvulinera bradyana, Elphidium crispum, Haynesina depressula</td>
</tr>
<tr>
<td>4. Soline Channel</td>
<td>Peneroplis pertusus, Peneroplis planatus</td>
<td>Quinqueloculina parvula</td>
</tr>
<tr>
<td>5. Križ (Open Sea)</td>
<td>Cibicides refugens</td>
<td>Asterigerinata mamilla, Gavelinopsis lobatulus</td>
</tr>
</tbody>
</table>

Table 5 Dominant and secondary species of benthic foraminifera in samples from each station. Surface sediment sample (0-2 cm), Mljet, May 1995.

Table 4 Benthic foraminiferal abundance. Surface sediment sample (0-2 cm), Mljet, May 1995 (numbers of stained individuals are given in the right column and numbers of unstained are given in the left column for each station).
assemblage is larger than the percentage of sessile specimens in the unstained association, contrary to the majority of vagile species.

5. DISCUSSION

As expected from physiographic and hydrographic data, the benthic foraminiferal assemblages show large differences. The ratio of Miliolina, Textulariina and Rotaliina (Table 6) indicates that the assemblages from stations located in the “lakes” (Stations #1 and 3) display characteristics of lagoon assemblages (MURRAY, 1995), whereas the assemblage at the marine nearshore station Križ (Station #5) indicates a normal marine environment with salinity over 30.

The smallest number of species and specimens in a standard 10 ml sample was found in Malo and Veliko Jezero (samples #1 and 3). Such assemblages are oligospecific (showing low species diversity and low abundance), but at the same time have high species dominance. Generally, they indicate a specific, restricted environment with stressed conditions (oxygen depletion, unusual temperatures, low or high salinity or their large variations). SEN GUPTA & MACHAIN-CASTILLO (1993) found that in dysoxic conditions typically 2-3 species constitute up to 80% of the total assemblage. We infer that the primary limiting factor for low species abundance, low species diversity, and high dominance in the Mljet Lakes is episodic low oxygen concentration (Table 1). The oxygen depletion of bottom water is produced by density stratification; in Malo Jezero the thermocline occurs between 5 and 12 m depth and in Veliko Jezero between 12 and 22 m depth. Both samples show that the fauna have three species making up to 64% of the total (unstained and stained) assemblage: H. depressula, V. bradyana and A. tepida represent 64% of total assemblage in sample #1; A. mamilla, V. bradyana and E. crispum make 63% of total assemblage in sample #3. In these samples the second dominant species is V. bradyana (making up to 15% of total assemblage at each station), an oxygen deficiency tolerant species (JORISSEN, 1987, p. 32). This species is absent in samples #4 and 5.

The species diversity index $H$ for total (stained and unstained) assemblages increases from about 0.8 in sample #1 to 1.4 in sample #5. Lower values found in samples #1, 2 and 3 are the result of a high dominance of very few species (Table 5). The highest value (sample #5) implies that more favourable conditions for foraminiferal diversity exist in the open marine environment. The equitability index $E$ is very low ranging from 0.18 in sample #2 to 0.26 in sample #5. This implies that all the samples are from somehow restricted environments.

Reoxygenation of bottom water after episodic deficiencies in the Mljet Lakes, as in other environments, is followed by colonization of benthic foraminifera. Shallow water foraminifera require only about three weeks to colonize the substrate and to stabilize their density (BUZAS, 1993, p. 158). Amongst many genera, representatives of Quinqueloculina and Elphidium are considered to be colonization pioneers. Their presence in all samples does not allow determination of whether foraminifera lived through the low oxygen/anoxia events, or if they recolonized after. However, in the Malo Jezero sample #1, the ratio between quinqueloculids and elphidiids (0.18:0.05) is similar to that known from an assemblage found at 1 m depth in experimental conditions in Florida (0.35:0.07 – BUZAS, 1993, p. 159). The different ratio in the Veliko Jezero sample #3 (0.02:0.21) probably reflects somewhat different conditions (greater depth, diminished turbulence, no algal cover, lower temperature) which are favorable for elphidiids.

The tendency of changing shell shape with depth has been observed as intraspecific variation in operculinae (PECHEUX, 1995). The morphological changes have been described either as thinning of the walls, or as a change in chamber proportions (HOTTINGER, 1997). In lamellar-perforate foraminifera the thinning of the chamber walls has been shown to be the result of diminishing rates of turbulence in the water column (REISS & HOTTINGER, 1984).

The distribution of the morphotypes of E. crispum in the Mljet Lakes coincides with differences in the nature of substrate. Muddy sediments with a high food concentration (samples #2, 3) host prevalently large, flattened, morphotype #1, whereas in a sandy substrate (samples #4, 5) smaller, inflated, morphotype #2 (with diameters about 40% smaller than those of morpho-

<table>
<thead>
<tr>
<th>SAMPLE</th>
<th>SHANNON-WIENER INDEX (H)</th>
<th>EQUITABILIT Y INDEX (E)</th>
<th>TEXTULARINA NUMBER</th>
<th>PERCENTAGE OF Miliolina NUMBER</th>
<th>ROTALIINA NUMBER</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Malo Jezero</td>
<td>0.81</td>
<td>0.22</td>
<td>0</td>
<td>0</td>
<td>30</td>
</tr>
<tr>
<td>2. Malo More</td>
<td>0.91</td>
<td>0.18</td>
<td>1</td>
<td>0.1</td>
<td>694</td>
</tr>
<tr>
<td>3. Veliko Jezero</td>
<td>0.97</td>
<td>0.23</td>
<td>1</td>
<td>0.68</td>
<td>12</td>
</tr>
<tr>
<td>4. Soline Channel</td>
<td>1.12</td>
<td>0.23</td>
<td>0</td>
<td>0</td>
<td>1265</td>
</tr>
<tr>
<td>5. Križ (Open Sea)</td>
<td>1.48</td>
<td>0.26</td>
<td>11</td>
<td>1.26</td>
<td>272</td>
</tr>
</tbody>
</table>

Table 6 Shannon-Wiener index, equitability index, and percentage of Textulariina, Miliolina and Rotaliina, Mljet, May 1995.
types # 1) prevails. This contrasts JORISSEN’s (1988) finding from the northern Adriatic Sea, where large, compact, morphotypes prevail in nutrient-poor conditions, and inflated morphotype in nutrient-rich conditions. On the other hand, this goes along with experimental evidence (TER KUILE & EREZ, 1988) that in lamellar perforate foraminifera the thinning of the chamber walls is a result of thinning of each lamella due to the diminishing rates of turbulence with increase in depth.

MURRAY (1991) suggested that elphidiids from a muddy substrate have infaunal preferences, while those from sand are more likely to have an epifaunal preference. LANGER (1988) and KITAZATO (1988) have described an epiphytic mode of life for *E. crispum* specimens, while MYERS (1943) noted that larger *E. crispum*, buried to a depth of about 1 cm, are able to escape in about 1 hour (calculation is made after Myers data, where active individuals spend about 12 hours traversing distance of 9 to 12 cm in vertical direction). It is expected that interstitial water in subsurface sediment (at one cm depth) has lower oxygen concentration than water at the water/sediment interface. Therefore, thinner, larger specimens (morphotype # 1) prefer muddy sediment with calm water above (Table 1; Fig. 2).

The relative sediment accumulation (relative sedimentation rate) can be estimated by using the percentage of sessile species, because attached species are incompatible with large sediment input (POAG et al., 1980). There is a net increase of the percentage of specimens of sessile species from Malo Jezero (absent) toward the open sea (Station #5, Križ) (Fig. 3). It suggests a greater sedimentation rate in the “lakes” than in open waters. The “lakes” most probably act as a trap for terrigenous and authigenous particles due to their topography.

*Haynesina depressula* is one of the most abundant species in bottom sediments of both Malo Jezero and Veliko Jezero. MURRAY (1991, p. 324), in an ecological overview of foraminifera, has representatives of genus *Haynesina* as brackish forams (living in salinity between 0 and 30), although (ibid, p. 141) some species can survive higher salinity (0-35). At the Malo Jezero, Malo More and Veliko Jezero stations stained specimens were noticed, indicating that those specimens were most probably authigenic. At the open-sea Križ station, *H. depressula* was not recorded, although hydrographic conditions, except for oxygen concentration, are similar to those in the “lakes”. The percentage of *H. depressula*, similarly to *V. bradyana*, in the association decreases towards the open sea, whereas at the same time the biodiversity increases. Most probably, *H. depressula* tolerates stress conditions including a large range of oxygen concentrations, salinity and temperature, but is probably a bad competitor. The lack of *H. depressula* at the Križ station might therefore be a consequence of the increased competition there.

6. CONCLUSIONS

This study is based on five surface sediment samples collected in May, 1995, from the Mljet Lakes, and therefore can be considered only as a preliminary note. However, it is possible to put forward the following conclusions:

1. Benthic foraminiferal assemblages from the Lakes area and from the nearshore indicate a transition from lagoonal towards open marine conditions, based on the ratio between Textulariina, Miliolina and Rotaliina.

2. The “lakes” behave as temporary hypoxic lagoons, in which the main limiting factor for the benthic foraminifera is oxygen concentration. Episodic stagnant conditions in Malo and Veliko Jezero are
formed due to large temperature and salinity differences between bottom and surface water, which prevents water mixing. At the same time the “lakes” act as sediment traps with a higher sedimentation rate compared to the adjacent open sea. Episodic anoxia is reflected in a low foraminiferal species diversity, high abundance of specimens of two pioneer genera (*Quinqueloculina* and *Elphidium*), and presence of *Valvulineria* species tolerant to low oxygen conditions.

(3) The number of species and specimens in sediment foraminiferal assemblages increases with the influence of the open sea. In these peculiar marine lakes, unstable ecological conditions do not permit the accommodation of either a large number of species or of specimens, whereas in the nearshore, where ecological conditions are more stable (“normal”), the assemblage is much richer in species. The Shannon-Wiener index is rather low in all samples suggesting restricted environment (H = 0.8 - 1.4), although its value increases continuously from the Malo Jezero towards the Kriz Station.

(4) The distribution of morphotypes of *Elphidium crispum* in the Mljet Lakes may be correlated to substrate type, mode of life, water energy, and oxygen conditions. The larger flattened specimens of morphotype #3 occur more commonly in a muddy, oxygen depleted, and low energy environment.

(5) In the study area, *Haynesina depressula* tolerates a salinity range significantly higher than previously documented. It appears to be well adapted to stressed conditions, but probably cannot tolerate competition.

Acknowledgments

The authors wish to thank the Mljtet National Park authorities for financial support for field research, Dr. Ivan Sondi for help in sampling, Miss Renata Slavkovic for technical assistance. We also thank to the referees Prof. dr. Ivan Gušić and Dr. Franc Cimerman for their helpful comments.

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Manuscript received June 6, 2000.
Revised manuscript accepted November 13, 2000.