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A review of research on the *Lemanea* genus in Serbia

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Abstract

The first data on the *Lemanea* genus in Serbia come from the late 20th century. Only one species, *L. fluviatilis*, was reported from 10 localities in Serbian riverine ecosystems between 1991 and 2017. Extensive research on this genus was performed in April–November 2017–2019, surveying 150 localities in 97 upland and mountain rivers. During this study period, the *Lemanea* genus was recorded at 14 localities in 12 rivers, while it disappeared from five previously reported localities. A total of four taxa were identified: *Lemanea fucina*, *L. rigida*, *Lemanea* sp. and *L. fluviatilis*. *Lemanea fucina* and *L. rigida* were recorded in Serbia for the first time. *L. fluviatilis* was the most common taxon. Our research confirmed that *Lemanea* species prefer similar specific environmental conditions. These species were found in temperate, soft or moderately hard, well-oxygenated and weakly alkaline waters, with low, moderate or high conductivity, and in waters with low content of inorganic nutrients. Due to their sensitivity to changes in environmental conditions, *Lemanea* species are exposed to negative anthropogenic impact leading to the degradation of their habitats. Intensive construction of small hydropower plants has threatened most habitats of the Rhodophyta species in the last few years.

Key words: *Lemanea fluviatilis*, *Lemanea fucina*, *Lemanea rigida*, morphology, ecology, distribution, negative anthropogenic impact

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1. Introduction

Identification of *Lemanea* species based on morphological features is very difficult due to multiple morphological variations, but also due to the fact that there are many synonyms in the literature (Kumano 2002; Eloranta et al. 2011). According to the available literature (Vis & Sheath 1992; Kumano 2002; Eloranta et al. 2011), differences between *Lemanea* species are based on diacritic features, mainly the length and width of the thallus, the way the sterile basal part transitions into the fertile part, branching, the arrangement of spermatangial papillae, the presence of the *Chantransia* stage, the length and diameter of *Chantransia* cells.

According to AlgaeBase (Guiry & Guiry 2020), 18 species of the genus *Lemanea* were flagged as taxonomically accepted based on morphological and reproductive features and molecular analysis. Eight of them were recognized in Europe: *L. borealis* Atkinson, *L. ciliata* (Sirodot) De Toni, *L. condensata* Israelson, *L. fluviatilis* (Linnaeus) C. Agardh, *L. fucina* Bory, *L. mamillosa* Kützing, *L. rigida* (Sirodot) De Toni and *L. sudetica* Kützing (Eloranta et al. 2011).

Most common species of the *Lemanea* genus is *L. fluviatilis*, which until now was the only species identified in Serbia (Simić 1995; 2002; 2007; Simić & Ranković 1998; Blagojević et al. 2017). The first data on the *Lemanea* genus in Serbia come from the late 20th century (Simić 1995). The first occurrence of *L. fluviatilis* was reported in 1991 in the Golema River (as the Crnovrška River; Simić 1995). Between 1991 and 2017, only *L. fluviatilis* was reported from 10 localities in seven upland and mountain rivers of Eastern (the Golema River, the Svrljiški Timok River, the Resava River and the Dojkinačka River) and Southern (the Vlasina River, the Božica River) Serbia (Simić 1995; 2002; 2007; Simić & Ranković 1998; Blagojević et al. 2017). These localities are characterized by specific ecological conditions (stable substrate in clean, cold, and temperate, fast-flowing, weakly alkaline and well-oxygenated waters). Although most of these habitats are protected to varying degrees, they are still affected by negative human impact (Simić et al. 2010).

Lemanea species are known to be stenovalent in relation to a large number of biotic and abiotic parameters. Any change in environmental conditions can lead to changes in the water regime and changes in ecological conditions in microhabitats where these sensitive species cannot continue to live (Eloranta & Kwandrans 2007; Simić et al. 2010; Eloranta 2019).

There are many factors that threaten habitats of *Lemanea* species (Eloranta & Kwandrans 2007; Simić et al. 2010). However, a major problem of habitat degradation is the intensive development of hydropower plants (HPPs), which has emerged in recent years. In order to reduce greenhouse gas emissions and mitigate climate change, the European Union established the EU Renewable Energy Directive, with HPPs as the global primary source of renewable energy (Berga 2016). HPPs are under development in all European countries, but the most dynamic development is observed in Central and Western Europe, in the Danube and Balkan regions (Schwarz 2019). Most of the HPPs are small and contribute only marginally to hydropower production (Manzano-Agugliaro et al. 2017). The most significant difference between large and small HPPs is that small HPPs are usually constructed on smaller rivers, unlike large HPPs (Kibler & Tullos 2013). Small HPPs have unavoidable negative environmental impacts, such as river fragmentation, modification of downstream hydromorphology, flow regimes, temperature, sediment transport and deposition (Liermann et al. 2012; Wiatkowski & Tomczyk 2018). The transformation of flowing rivers into standing water can have multifarious effects on primary production and changes in benthic organisms (Wu et al. 2010). Negative ecological consequences of small HPPs are recognized in many countries, resulting in their removal. In the Balkan region, the development of HPPs, especially small HPPs, is increasing. More than 3800 HPPs are planned to be constructed or are currently under construction directly on the mountain, pristine Balkan rivers characterized by the richest biodiversity (Schwarz 2019; Hunđek et al. 2020).

This paper aims to present a review of research on the *Lemanea* genus in Serbian riverine ecosystems and to provide new data on the diversity of *Lemanea* species in Serbia, their morphology, distribution and ecology, based on the analysis of 14 populations found in Serbian rivers. Possible factors threatening the habitats of *Lemanea* species are presented and discussed, including mainly the negative environmental impact of small HPPs.

2. Materials and methods

2.1. Sample collection

Field surveys were conducted at 150 localities in 97 rivers of Western, Southwestern, Eastern and Southern Serbia from April to November in 2017, 2018 and 2019. Twenty mature thalli were collected at each locality where *Lemanea* taxa were found. In addition to thalli of *Lemanea*, thalli of other macroalgal aggregations were collected. Samples of algae were collected at a depth ranging from 0 to 50 cm by scraping them from the stony substrate with tweezers. The collected material was immediately preserved with 4% formaldehyde or 96% ethanol. The percentage cover of *Lemanea* species was assessed by visual analysis for each 1 m section and averaged for 10 m lengths along the riverbed (Necchi & Moreira 1995; Ramirez-Rodriguez et al. 2007). All collected samples are stored in the collection of the Department of Biology and Ecology, Faculty of Science, University of Kragujevac.

2.2. Microscopic observation and species identification

Morphological features were analyzed under a Motic BA310 microscope with up to 800× magnification and photographed with BRESSER (9MP) and MicroCamLab. For the identification of *Lemanea* species, the following morphological and reproductive features were recorded and measured: thalli length, presence of a stalked sterile basal part and its transition into the fertile part of the thallus, presence and frequency of branching, nodal diameter (ND), internodal diameter (ID), nodal/internodal diameter ratio (ND/ID), spermatangial papillae arrangement, length and diameter of carpospores, as well as the presence of the *Chantransia* stage. *Lemanea* species were identified according to Kumano (2002), Eloranta & Kwandrans (2007) and Eloranta et al. (2011). Other algae present in the collected samples were identified according to Krammer & Lange-Bertalot (1986, 1991), Komárek & Anagnostidis (1995, 2005), Komárek (2013) and Wehr & Sheath (2003).

2.3. Environmental conditions

The type of substrate, current velocity (m s^{-1}), maximum depth and shade were determined at each locality. Environmental conditions were measured according to the American Public Health Association (1995): temperature (°C), pH, conductivity (µS cm^{-1}), water hardness (mg l^{-1}), dissolved oxygen (mg l^{-1}) and nutrient concentration. Nitrogen concentration was determined as ammonia nitrogen NH_4-N (mg l^{-1}) and nitrate nitrogen NO_3-N (mg l^{-1}), while the concentration of soluble phosphorus was determined as orthophosphate PO_4-P (mg l^{-1}) concentration.

Possible threat factors were determined at each locality by visual analysis, as well as according to the Survey of Small Hydropower Plants in the Republic of Serbia (Ministry of Mining and Energy of the Republic of Serbia): 1 – no negative impact, 2 – impact by local population (wastewater, solid waste, traffic), 3 – planned construction of HPP, 4 – small HPP constructed , 5 – planned construction of small HPP.

2.4. Literature review

The available literature on the distribution and ecology of the *Lemanea* genus in Serbia published between 1995 and 2017 was compiled and reviewed.

3. Results

During field surveys carried out in 2017, 2018, and 2019, a total of 150 riverine locations were studied and thalli of the *Lemanea* genus were collected from 14 locations in 12 rivers (Fig. 1, Tables 1, 2). Six of them were already known from previous studies (the Golema River, the Dojkinačka River – three localities, the Božica River and the Vlasina River), while eight of

Figure 1

Geographical location of *Lemanea fucina*, *Lemanea rigida*, *Lemanea* sp. and *Lemanea fluviatilis* localities in Serbia

(■) *Lemanea fucina*: the Veljušnica River (VE); (♣) *Lemanea rigida*: the Jelašnica River (JR), the Gradska River (GR), the Božica channel (BC); (▲) *Lemanea* sp.: the Masurica River (MR), the Vuneva River (VU); (●) *Lemanea fluviatilis*: the Veliki Rzav River (VR), the Mileševka River (MI), the Vlasina River (VL), the Božica River (BR), the Golema River (GO), the Dojkinačka River (DR)

Table 1

Geographical coordinates and environmental parameters of *Lemanea fucina*, *Lemanea rigida* and *Lemanea* sp. localities in Serbia

Species	River (population code)/Date	Geographical coordinates	Altitude (m)	Depth (cm)	Substrate type	Velocity (m s^{-1})	Temperature (°C)	pH	Cond. (µS cm^{-1})	Hardness (mg l^{-1})	O_2 (mg l^{-1})	NH_4 (mg l^{-1})	NO_3 (mg l^{-1})	PO_4 (mg l^{-1})	Degree of shade	Coverage (%)	Associated macroalgae	Threat factors
Lemanea fucina	Veljušnica (VE) 15.08.2018	43°22′05.7″N 19°54′35.0″E	992	0	stone	1.3	13.9	8.11	320	160	9.87	<0.03	<4	<0.06	++	20	*Cladophora glomerata*	2
Lemanea rigida	Jelašnica (JR) 20.08.2019	42°37′56.9″N 22°07′06.6″E	433	5-10	stone	1.5	17.4	7.53	590	280	9.72	<0.03	<4	<0.06	++	10	*Paralemanea* sp.	2
	Gradska River (GR) 26.05.2018	42°54′07.6″N 22°20′46.3″E	544	0	stone	1.8	14.7	7.51	100	50	9.96	<0.03	<4	0.19	+++	10	*Nostoc* sp.	2, 4
	Božica channel (BC) 23.07.2019	42°40′44.8″N 22°21′02.1″E	1212	0-5	stone	2	15.6	7.7	510	260	9.66	<0.03	<4	<0.06	+++	10	*Audouinella hermannii* *Hydrurus foetidus* *Cladophora glomerata*	2
Lemanea sp.	Masurica (MR) 28.05.2018	42°36′48.5″N 22°13′13.0″E	887	5-10	stone	1.5	11.5	7.48	60	30	10.35	<0.03	<4	<0.06	++	30	/	1
	Vuneva (VU) 28.05.2018	42°36′46.7″N 22°13′16.2″E	889	10	stone	1.3	11.2	7.46	70	30	10.41	<0.03	<4	<0.06	+	7	/	1

+++ full sunlight; ++ partial shade; + full shade.

1 – no negative impact; 2 – impact by local population (wastewater, solid waste, traffic); 3 – planned construction of HPP; 4 –small HPP constructed; 5 – planned construction of small HPP

Table 2

Geographical coordinates and environmental parameters of *Lemanea fluviatilis* localities in Serbia

Species	River (population code)/Date	Geographical coordinates	Altitude (m)	Depth (cm)	Substrate type	Velocity (m s^{-1})	Temperature (°C)	pH	Cond. (µS cm^{-1})	Hardness (mg l^{-1})	O_2 (mg l^{-1})	NH_4 (mg l^{-1})	NO_3 (mg l^{-1})	PO_4 (mg l^{-1})	Degree of shade	Coverage (%)	Associated macroalgae	Threat factors
Lemanea fluviatilis	Veliki Rzav (VR)* 19.05.2018	43°45′12.5″N 22°00′12.1″E	389	50	stone	2.0	10.4	7.98	270	130	9.98	<0.03	<4	<0.06	+++	5	*Nostoc* sp.	3
	Mileševka (MI)* 06.07.2019	43°21′58.4″N 19°43′16.9″E	571	5	stone	1.6	15.1	8.05	295	150	9.91	<0.03	<4	<0.06	++	10	*Nostoc* sp. *Cladophora glomerata*	2
	Vlasina (VL) 26.05.2018	42°51′09.4″N 22°17′02.1″E	730	0-5	stone	1.5	14.1	7.59	90	40	10.1	<0.03	<4	<0.06	+++	20	*Nostoc* sp. *Hydrurus foetidus* *Cladophora glomerata*	2, 4, 5
	Božica River (BR) 27.05.2018	42°37′07.0″N 22°24′02.4″E	1038	0	stone	1.3	13.3	7.08	80	40	9.35	<0.03	<4	0.21	+++	20	*Hydrurus foetidus*	2
	Golema River (GO) 30.08.2018	43°23′44.2″N 22°36′18.8″E	905	0	stone	1.5	13.6	7.83	180	100	9.86	<0.03	<4	<0.06	+	30	/	2
	Dojkinačka River (DR1) 19.08.2019	43°15′40.9″N 22°46′50.6″E	960	10	stone	2.0	12.1	7.32	160	100	10.31	<0.03	<4	<0.06	+	10	/	5
	Dojkinačka River (DR2) 19.08.2019	43°15′02.0″N 22°46′32.6″E	972	10	stone	1.5	12.3	7.26	140	110	10.2	<0.03	<4	<0.06	++	20	/	5
	Dojkinačka River (DR3) 19.08.2019	43°15′32.0″N 22°46′37.8″E	924	10	stone	1.8	12.3	7.29	140	110	10.28	<0.03	<4	<0.06	++	20	/	5

* new finding

+++ full sunlight; ++ partial shade; + full shade.

1 – no negative impact; 2 – impact by local population (wastewater, solid waste, traffic); 3 – planned construction of HPP; 4 – small HPP constructed; 5 – planned construction of small HPP

them represent new localities in Serbia (the Veljušnica River, the Jelašnica River, the Gradska River, the Božica channel, the Masurica River, the Vuneva River, the Veliki Rzav River and the Mileševka River; Fig. 1). Four taxa were identified at 14 localities: *Lemanea fucina*, *L. rigida, Lemanea* sp. and *L. fluviatilis*. Thalli of *L. fucina* and *L. rigida* were recorded in Serbia for the first time. Morphological features of the thalli collected from the Masurica River and the Vuneva River did not match those described in recent identification keys.

Geographical coordinates and environmental parameters of the *Lemanea* localities are summarized in Tables 1 and 2. Morphological and reproductive features of the identified *Lemanea* taxa are summarized in Tables 3 and 4.

Our research covered all previously known localities of *Lemanea* species (10 localities) in Serbia. We found that this genus disappeared from four of them (two localities in the Resava River, one locality in the Svrljiški Timok River and one locality in the Dojkinačka River). Geographical coordinates and environmental data from previous research on *Lemanea* are presented in Table 5.

Hypertrophies of tissue at the base of spermatangia, in the form of papules with regular or irregular edges, were observed along thalli collected from the Božica River, the Dojkinačka River, the Veljušnica River, the Jelašnica River and the Gradska River.

3.1. ***Lemanea fucina*** Bory 1808

Homotypic synonym: *Sacheria fucina* (Bory) Sirodot

Heterotypic synonym: *Lemanea mamillosa* var. *fucina* Kützing

Morphological features

Thalli grew in tufts. Almost every collected thallus was tattered and small in size, very dark green or black in color, and covered with the epiphyte *Leptolyngbya foveolarum* (Gomont) Anagnostidis and Komárek. The length of such thalli ranged from 3.2 to 4.5 cm (Fig. 2: 1, Table 3). False branching was observed in most of the regenerated parts of such thalli (Table 3). Few thalli collected from the same population were delicate, light green with clearly visible abundant branching (Fig. 2: 1, Table 3) and without epiphytes. The length of such thalli ranged from 7.6 to 8.7 cm (Fig. 2: 1, Table 3). The thalli gradually narrowed toward the base and continued into the sterile basal part (Fig. 2: 2, Table 3). The sterile basal part was 0.8–2.85 cm long, thin, slightly stalked. The nodal diameter (ND) ranged from 460 to 690 µm and the internodal diameter (ID) ranged from 370 to 560 µm (Fig. 2: 3, Table 3). The ratio of nodal diameter to internodal diameter (ND/ID) was 1.3 (Table 3). Spermatangial papillae were protruding, 2–3 in whorls, regularly or irregularly distributed in the

Table 3

Morphological and reproductive features of *Lemanea fucina*, *Lemanea rigida* and *Lemanea* sp. from Serbia

Species	River	Plant length (cm)	Sterile basal part	Branching	Nodal diameter (µm)	Internodal diameter (µm)	ND:ID	Spermatangial papillae arrangement	Carpospores length (µm)	Carpospores diameter (µm)	*Chantransia*
Lemanea fucina	Veljušnica (VE).	3.2–8.7	gradually expanding into the fertile part	true/false	460–690	370–560	1.3	Protruding; 2–3 in whorls; regular or irregular	15.2–19.1 (29.5–48.8)*	9.6–13.8 (20.5–42.6)*	+
Lemanea rigida	Jelašnica (JR)	5.3–8.5	gradually expanding into the fertile part	true	480–720	300–450	1.4	protruding or flat; 2–3 in whorls; regular or irregular	26.8–42.1*	19.3–33.2*	–
	Gradska River (GR)	5.1–9.25	gradually expanding into the fertile part	true/false	410–590	300–430	1.4	protruding or flat; 3 in whorls; regular or irregular	13.6–20.5	10–15.2	–
	Božica channel (BC)	4.6–9.7	gradually expanding into the fertile part	true/false	490–750	400–580	1.3	protruding or flat; 2–3 in whorls; regular or irregular	30.7–42.1*	20.5–30.7*	–
Lemanea sp.	Masurica (MR)	2.3–5	imperceptibly expanding into the fertile part	true	360–530	290–440	1.3	plane, rarely protruding; 2–3 in whorls; regular or irregular	12.1–22.5	6.2–13.5	–
	Vuneva (VU)	2.6–5.6	imperceptibly expanding into the fertile part	true	380–520	300–440	1.3	plane, rarely protruding; 2–3 in whorls; regular or irregular	12–22	6–13.7	–

+ present; – not present
*mature carpospores

Table 4

Morphological and reproductive features of *Lemanea fluviatilis* from Serbia

Species	River (population code)	Plant length (cm)	Sterile basal part	Branching	Nodal diameter (µm)	Internodal diameter (µm)	ND:ID	Spermatangial papillae arrangement	Carpospores length (µm)	Carpospores diameter (µm)	*Chantransia*
Lemanea fluviatilis	Veliki Rzav (VR)	2.5–5.2	abruptly expanding into the fertile part	true/false	400–570	290–440	1.5	patches; 2–3 in whorls; regular or irregular	21.7–31.2	12.1–17.5	–
	Mileševka (MI)	4.5–11.5	abruptly or gradually expanding into the fertile part	true/false	450–590	300–430	1.4	protruding; 2–4 in whorls; regular or irregular	35.8–50.5*	20.5–38.5*	+
	Vlasina (VL)	4.9–12.2	abruptly expanding into the fertile part	true/false	550–680	400–550	1.3	patches; 2–3 in whorls; regular or irregular	20.5–33.7	13.6–18.8	–
	Božica River (BR)	4.7–7.1	abruptly expanding into the fertile part	true	460–650	350–520	1.3	patches; 2–3 in whorls; regular or irregular	23.5–33.5*	15.2–20.5*	+
	Golema River (GO)	4.7–6.2	abruptly expanding into the fertile part	true/false	500–620	360–450	1.3	patches; 2–4 in whorls; regular or irregular	20.5–26.2	10.8–18.5	–
	Dojkinačka River (DR1, DR2, DR3)	5.4–9.3	abruptly expanding into the fertile part	no	510–780	360–580	1.4	patches; 2–3 in whorls; regular or irregular	29.5–41*	18.5–25.3*	+

+ present; – not present

*mature carpospores

nodal region (Fig. 2: 3, Table 3). The carposporophyte zone was usually cylindrical. Young carpospores occurred in strings, cylindrical (length 15.2–19.1 µm, width 9.6–13.8 µm; Table 3). Mature carpospores were oval to oblong (length 29.5–48.8 µm, width 20.5–42.6 µm; Table 3). The *Chantransia* stage was present in places where the thallus was torn (Table 3), branched unilaterally and alternately. Monospores were not observed. The sporophyte develops from the *Chantransia* stage.

Table 5

Geographical coordinates and environmental parameters of the previously described *Lemanea fluviatilis* localities from Serbia

River (population code)/Date	Geographical coordinates	Altitude (m)	Depth (cm)	Substrate type	Velocity (m s^{-1})	Temperature (°C)	pH	Conductivity (µS cm^{-1})	O_2 (mg l^{-1})	N (mg l^{-1})	P (mg l^{-1})	Degree of shade	Associated macroalgae	Reference
Golema River (as the Crnovrška River) 06.1991	/	1250	/	stone	1.42	9.0	7.6	/	13.6	0.45	0.2	++	*Chamaesiphon polonicus* *Phormidium favosum* *Tapinothrix janthina* (as *Homoeothrix janthina*)	Simić 1995
Svrljiški Timok River 06.1991	/	400	/	stone	1	14.7	8.35	/	10.68	0.45	0.1	+++	*Chantransia pygmaea* *Vaucheria* sp. *Cladophora glomerata* *Stigeoclonium elongatum* *Ulothrix zonata*	Simić 2002
Resava River 01.05.2003	/	450	/	/	1.5	/	/	/	/	/	/	/	/	Simić 2007
Resava River 12.04.2004	/	800	/	/	1.1	10.0	7.8	160	8.59	4.7	0.058	/	/	Simić 2007
Božica River 15.08.2004	/	1100	/	/	1.1	13.8	7.1	70	8.51	4.6	0.443	/	/	Simić 2007
Vlasina River 15.08.2004	/	1000	/	/	/	/	/	/	/	/	/	/	/	Simić 2007
Dojkinačka River 26.07.2010	43°15′43.3″N 22°46′23.2″E	1015	30	/	/	12.5	7.0	/	/	/	/	/	/	Blagojević et al. 2017
Dojkinačka River 25.07.2010	43°15′24.5″N 22°46′31.3″E	1000	30	/	/	15.0	7.5	/	/	/	/	/	/	Blagojević et al. 2017
Dojkinačka River 25.07.2010	43°15′02.0″N 22°46′32.6″E	972	30	/	/	16.0	8.0	/	/	/	/	/	/	Blagojević et al. 2017
Dojkinačka River 25.07.2010	43°15′32.0″N 22°46′37.8″E	924	30	/	/	17.0	7.0	/	/	/	/	/	/	Blagojević et al. 2017

+++ full sunlight; ++ partial shade

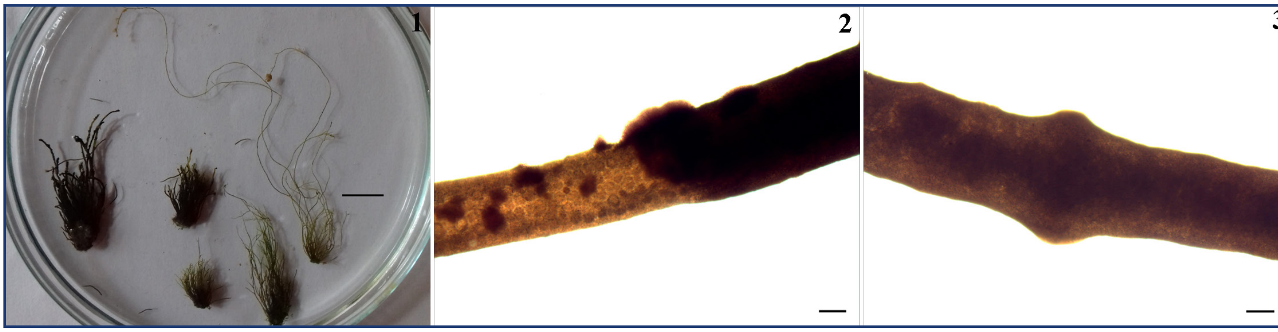

Figure 2

Morphological and reproductive features of *Lemanea fucina*: 1 – habit; 2 – transition of the sterile basal part into the fertile part; 3 – nodal and internodal diameter, spermatangial papillae arrangement. Scale bars: 1 cm for plate 1; 100 µm for plates 2 and 3

3.2. ***Lemanea rigida*** (Sirodot) De Toni 1897

Basionym: *Sacheria rigida* Sirodot

Heterotypic synonym: *Lemanea fucina* var. *rigida* Atkinson

Morphological features

Thalli grew in tufts. Their length ranged from 4.6 to 9.7 cm (Fig. 3: 1, Table 3). They were dark green in color. The thalli gradually narrowed into the base and continued into the sterile basal part (Fig. 3: 2, Table 3). The sterile basal part was 0.4–1.6 cm long, thin, slightly stalked. True branching was present, but not abundant (Table 3). False branching was observed in the regenerated parts of the thallus in places where it was torn (the Gradska River and the Božica channel; Table 3). The nodal diameter (ND) ranged from 410 to 750 µm and the internodal diameter (ID) ranged from 300 to 580 µm (Fig. 3: 3, Table 3). The nodal to internodal diameter ratio (ND/ID) ranged from 1.3 to 1.4 (Table 3). Spermatangial papillae were protruding or flat, 3 in whorls, regularly or irregularly distributed in the nodal region (Fig. 3: 3, Table 3). The carposporophyte zone was usually cylindrical. Young carpospores were in strings, oval to oblong (length 13.6–20.5 µm, width 10–15.2 µm; the Gradska River; Table 3). Oval to oblong mature carpospores (length 26.8–42.1 µm, width 19.3–33.2 µm) were observed in specimens from the Jelašnica River and the Božica channel (Table 3). The *Chantransia* stage was not observed (Table 3).

3.3. ***Lemanea*** **sp.**

Morphological features

Thalli grew in tufts. Their length ranged from 2.3 to 5.6 cm (Fig. 4: 1, Table 3). They were olive green to dark green, curved, slender. They indistinctly tapered toward the base and continued into the sterile basal part (Table 3). The sterile basal part was 0.5–0.9 cm

Figure 3

Morphological and reproductive features of *Lemanea rigida*: 1 – habit; 2 – transition of the sterile basal part into the fertile part; 3 – nodal and internodal diameter, spermatangial papillae arrangement. Scale bars: 1 cm for plate 1; 100 µm for plates 2 and 3

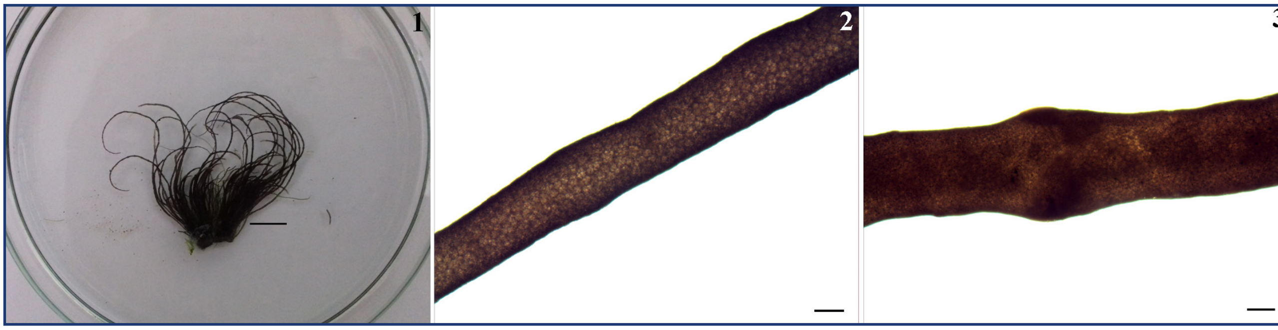

Figure 4

Morphological and reproductive features of *Lemanea* sp.: 1 – habit; 2 – transition of the sterile basal part into the fertile part; 3 – nodal and internodal diameter, spermatangial papillae arrangement. Scale bars: 1 cm for plate 1; 100 µm for plates 2 and 3

long, thin, unstalked. True branching was present (Table 3). The nodal diameter (ND) ranged from 360 to 530 µm and the internodal diameter (ID) ranged from 290 to 440 µm (Fig. 4: 2, Table 3). The nodal to internodal diameter ratio (ND/ID) was 1.3 (Table 3). Spermatangial papillae were flat, slightly or rarely prominently protruding, 2–3 in whorls, regularly or rarely irregularly distributed in the nodal region (Fig. 4: 3, Table 3). The carposporophyte zone was usually cylindrical. Young carpospores were in strings, ellipsoidal to oblong (length 12–22.5 µm, width 6–13.7 µm; Table 3). Mature carpospores and the *Chantransia* stage were not observed (Table 3).

3.4. ***Lemanea fluviatilis*** (Linnaeus) C.Agardh 1811

Basionym: *Conferva fluviatilis* Linnaeus

Homotypic synonyms: *Conferva fluviatilis* Linnaeus, *Chantransia fluviatilis* (Linnaeus) De Candolle, *Sacheria fluviatilis* (Linnaeus) Sirodot

Heterotypic synonyms: *Chantransia nigricans* De Candolle, *Lemanea corallina* Bory, *Lemanea fucina* var. *subtilis* Atkinson

Morphological features

Thalli grew in tufts. Their length ranged from 2.5 to 12.2 cm (Fig. 5: 1, Table 4). The thalli were yellowish olive or olive green in color. They abruptly narrowed toward the base and continued into the sterile basal part (Fig. 5: 2, Table 4). The sterile basal part was 0.5–1.5 cm long, thin, stalked. True branching was sparse; false branching was also observed (Table 4). The nodal diameter (ND) ranged from 400 to 780 µm and the internodal diameter (ID) ranged from 290 to 580 µm (Fig. 5: 3, Table 4). The nodal to internodal diameter ratio (ND/ID) ranged from 1.3 to 1.5 (Table 4). Spermatangial papillae occurred in patches, 2–4 in whorls, regularly or irregularly distributed in the nodal region (Fig. 5: 3, Table 4). The carposporophyte zone was usually cylindrical. Young carpospores were in strings, cylindrical (length 20.5–33.7 µm, width 10.8–18.8 µm; Table 4). Mature carpospores were oval to oblong (length 23.5–50.5 µm, width 15.2–38.5 µm; Table 4). The *Chantransia* stage was observed in specimens collected in the Mileševka River, the Božica River and the Dojkinačka River (Table 4). It branched unilaterally and alternately. Monospores were not observed.

3.5. Distribution and ecology

The most common species in the collected samples was *L. fluviatilis*, found at eight localities. *Lemanea rigida* was found at three localities, *L. fucina* at one locality, while *Lemanea* sp. was found at two localities. Thalli of *L. fluviatilis* were collected from the Veliki Rzav River, the Mileševka River (Southwestern Serbia), the Golema River and from three localities in the Dojkinačka River (Eastern Serbia), the Božica River and the Vlasina River (Southern Serbia; Fig. 1, Table 2). Thalli of *L. fucina* were collected from the Veljušnica River (Southwestern Serbia), while thalli of *L. rigida* were collected from the Jelašnica River, the Gradska River and the Božica channel (Southern Serbia; Fig. 1, Table 1). Thalli of *Lemanea* sp. were collected from the Masurica River and the Vuneva River (Southern Serbia) (Fig. 1, Table 1). These *Lemanea* taxa were found at altitudes ranging from 389 m to 1212 m in similar specific environmental conditions (Tables 1, 2). Thalli of *L. fucina*, *L. rigida*, *Lemanea* sp. and *L. fluviatilis* were found in turbulent lotic waters with

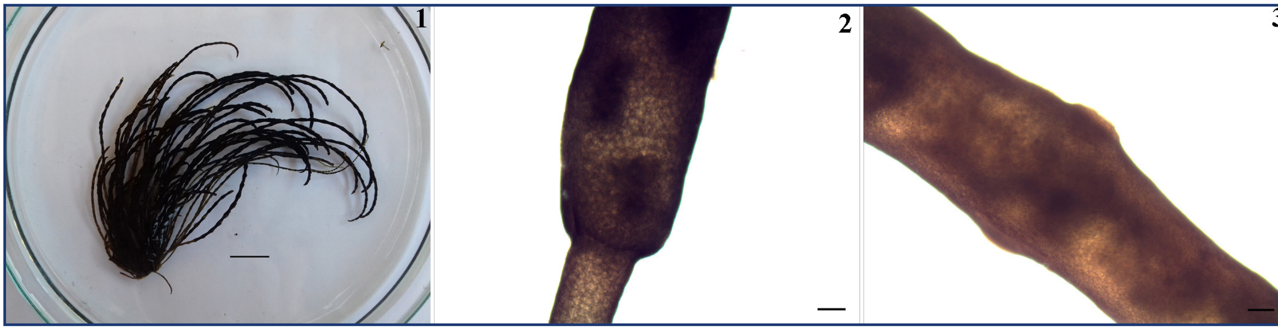

Figure 5

Morphological and reproductive features of *Lemanea fluviatilis*: 1 – habit; 2 – transition of the sterile basal part into the fertile part; 3 – nodal and internodal diameter, spermatangial papillae arrangement. Scale bars: 1 cm for plate 1; 100 µm for plates 2 and 3

current velocity ranging from 1.3 to 2 m s^{-1}, on the stony substrate at depths ranging from 0 to 50 cm, in full sunlight, in partial or full shade (Tables 1, 2). The water from which thalli were collected was temperate (water temperature ranging from 11.2°C to 17.4°C), soft or moderately hard (water hardness ranging from 30 mg l^{-1} to 280 mg l^{-1}), well-oxygenated (from 9.66 mg l^{-1} to 10.41 mg l^{-1}) and weakly alkaline (pH from 7.46 to 8.11), with low, moderate or high conductivity (from 60 µS cm^{-1} to 590 µS cm^{-1}) and low content of inorganic nutrients (Tables 1, 2). Only the concentration of orthophosphates was slightly increased at the localities in the Gradska River and the Božica River (Table 1).

Thalli of *Nostoc* sp. grew together with thalli of *L. rigida* (the Gradska River) and *L. fluviatilis* (the Veliki Rzav River, the Mileševka River and the Vlasina River). The alga *Cladophora glomerata* (L.) Kützing grew together with thalli of *L. fucina* (the Veljušnica River), *L. rigida* (the Božica channel) and *L. fluviatilis* (the Mileševka River and the Vlasina River), whereas thalli of *Paralemanea* sp. grew together with thalli of *L. rigida* (the Jelašnica River). The red alga *Audouinella hermannii* (Roth) Duby and the chrysophycean alga *Hydrurus foetidus* (Villars) Trevisan were found together with thalli of *L. rigida* in the Božica channel. The chrysophycean alga *H. foetidus* was also found growing together with thalli of *L. fluviatilis* in the Vlasina River.

Epiphytes were found on thalli of *Lemanea fucina, L. rigida* and *L. fluviatilis*. The cyanobacterial species *Chamaesiphon rostafinskii* Hansgirg, *L. foveolarum*, *L. notata* (Schmidle) Anagnostidis and Komárek and the diatom taxa *Gomphonella olivacea* (Hornemann) Rabenhorst and *Navicula* sp. developed as epiphytes on *L. fucina* thalli, while the cyanobacterial species *L. foveolarum*, the red alga *A. hermannii* and the diatom taxa *Cymbella* sp., *G. olivacea*, *Gomphonema capitatum* Ehrenberg, *Navicula* sp. and *Planothidium lanceolatum* (Brébisson ex Kützing) Lange-Bertalot developed as epiphytes on *L. rigida* thalli. The cyanobacterial species *Ch. rostafinskii* and the diatom species *Cocconeis placentula* Ehrenberg and *G. olivacea* developed as epiphytes on *L. fluviatilis* thalli.

3.6. Threat factors

It was observed during the field surveys that only the Masurica and Vuneva river localities were not affected by negative anthropogenic impact. Whereas all other localities were found to be affected by threat factors (Tables 1, 2).

4. Discussion

Our research confirms the difficulties in the identification of *Lemanea* species based on the morphological and reproductive features described in the available literature. Kučera & Marvan (2004) speculated that small variations in diacritic features could be a consequence of the variation in age and maturity of thalli.

The above-mentioned difficulties in identifying *Lemanea* species are particularly evident for *L. fucina* and *L. mamillosa*. In the literature, these two species were described under different synonyms, and the morphological and reproductive differences between them are often not clear enough (Kumano 2002; Eloranta et al. 2011). Simić & Đorđević (2011) observed congruence with the basic diagnostic features of these two species in the material collected from the same locality in the Tara River during the same period of the life cycle, but in different years. The identification of thalli collected from the Veljušnica River was quite difficult due to the small size of collected thalli, which is probably a consequence of grazing by herbivorous macroinvertebrates. Grazing can also explain damage to almost every collected thallus. According to Caro-Borrero and Carmona- Jiménez (2016), red algae can be used as a food source by herbivorous macroinvertebrates, which leads to the damage of thalli and increased release and germination of carpospores and new gametophytes.

False branching was observed on thalli of *L. fucina*, *L. rigida* and *L. fluviatilis* in places where thalli were torn. A similar phenomenon was described in *Paralemanea mexicana* (Kützing) M.L.Vis and R.G.Sheath (Vis & Sheath 1992; Carmona & Necchi 2002), based on which this species was distinguished from other *Paralemanea* species. False branching was also described in *P. annulata* (Kützing) M.L.Vis and R.G.Sheath and *P. catenata* (Kützing) M.L.Vis and R.G.Sheath (Simić & Đorđević 2017). Some authors suggested that false branching is apparently exclusive to *P. mexicana* (Carmona et al. 2013). However, we disagree that those newly formed branches are taxonomic features.

Since identification of *Lemanea* species based on morphological and reproductive features is difficult and insufficient, morphological analysis combined with molecular analysis is required for reliable identification.

Lemanea fluviatilis is the most common species of *Lemanea*. It has been studied by many authors and its ecology and distribution are fairly well researched. The species occurs mainly in the Northern Hemisphere, in Europe, North America and Asia (Vis, Sheath 1992; Eloranta et al. 2011; Ganesan et al. 2018). Based on previously published data as well as this paper, *L. fluviatilis* is the most frequent species of *Lemanea* in Serbia (Simić 1995; 2002; 2007; Simić & Ranković 1998; Blagojević et al. 2017). *Lemanea fucina* and *L. rigida* occur in Europe (Eloranta et al. 2011), while *L. fucina* is also recorded in North America (Vis & Sheath 1992).

Data on the geographical distribution and ecology of the *Lemanea* genus in the Balkan region are very scarce. With the exception of Serbia, rare *Lemanea* species were reported from Albania (Kashta & Miho 2016), Bulgaria (Temniskova et al. 2008), Croatia (Koletić et al. 2020) and Montenegro (Simić & Djordjević 2011; Simić et al. 2019). *Lemanea fucina* was recorded in Croatia (Koletić et al. 2020) and Montenegro (Simić & Djordjević 2011; Simić et al. 2019), *L. rigida* in Croatia (Koletić et al. 2020), while *L. fluviatilis* was also recorded in Croatia (Koletić et al. 2020). Our collections of *L. fucina* and *L. rigida* represent the first occurrence of these rare species in Serbia and contribute to the knowledge of their distribution and ecology in the Balkan region.

In general, *Lemanea* species occur in turbulent flowing waters. They colonize stable and hard substrates, such as stones, rocks, but also concrete blocks, bridge pillars and rarely wood, and occur in full sunlight or partially shaded rivers with high to moderate flow rates (Vis & Sheath 1992; Simić 1995; 2002; 2007; Eloranta & Kwandrans 1996; 2007; Chemeris & Bobrov 2009; Eloranta et al. 2016; Eloranta 2019). In our study, all thalli were collected from stony substrates, at places characterized by high flow rates (from 1.3 m s^{-1} to 2 m s^{-1}). Thalli of *L. fluviatilis* were found in full sunlight (the Veliki Rzav River, the Vlasina River and the Božica River), as well as in partial (the Mileševka River and the Dojkinačka River) and full shade (the Golema River and the Dojkinačka River). Thalli of *L. fucina* were found in partial shade, thalli of *L. rigida* were found in partial shade (the Jelašnica River) and full sunlight (the Gradska River and the Božica channel), while thalli of *Lemanea* sp. were found in full (the Vuneva River) and partial shade (the Masurica River).

Thalli of the *Lemanea* genus can be found at a depth of more than 100 cm, but they reach their maximum growth and development in early spring and summer when the water level is low and algae often remain on the rock surface within the contact zone between water and air (Vis & Sheath 1992; Eloranta & Kwandran 2007; Simić 1995; 2002; 2007). In our study, thalli of the *Lemanea* genus were found at a depth ranging from 0 to 50 cm.

Our research confirmed that *Lemanea* species prefer cold and temperate, soft or moderately hard, neutral or slightly alkaline, well-oxygenated and oligotrophic water (Vis & Sheath 1992; Simić 1995; 2002; 2007; Eloranta & Kwandrans 1996; 2007; Eloranta et al. 2016; Eloranta 2019). According to Dell'Uomo (1991), however, they can also be found in waters with moderate pollution.

Because *Lemanea* species are adapted to specific environmental conditions, any direct or indirect negative anthropogenic impact threatens their survival. Intensification of negative anthropogenic impact on the habitats of *Lemanea* species has led to *Lemanea* species being protected in many countries (Siemińska 1992; Temniskova et al. 2008; Hyvärinen et al. 2019). In Serbia, the *Lemanea* genus is not legally protected. According to the Code on declaration and protection of strictly protected and protected wild species of plants, animals and fungi, Appendix 1 (Institute for Nature Conservation of Serbia 5/2010, 47/2011, 32/2016, 98/2016), ten species of Rhodophyta from the genera *Bangia*, *Batrachospermum*, *Hildenbrandia*, *Paralemanea*, and *Thorea* are protected in Serbia.

Previous findings on the occurrence of *L. fluviatilis* in the Svrljiški Timok River (Simić 2002), the Resava River (two localities; Simić 2007) and the Dojkinačka River (Lilina česma locality; Blagojević et al. 2017) were not confirmed by this research. The locality in the Svrljiški Timok River was affected by eutrophication. One locality at the Resava River was destroyed in a wildfire, while the negative impact of the local community (wastewater, solid waste) was observed at the other locality in the same river. The riverbed at one locality in the Dojkinačka River was dry during the sampling period.

Habitats of the new *Lemanea* species are exposed to the impact of the local community (wastewater, solid waste, traffic), and several of them may be threatened by the development of HPPs, usually the derivative type of small HPPs.

The construction of all planned small HPPs in Serbia will provide an insignificant energy balance, but environmental damage to these ecosystems will be immeasurable (Ristić et al. 2018). Since all parts of riverine ecosystems are interconnected, any disturbance to one part of the system will trigger a response in most parts of the system (Wu et al. 2010). The significant impact of small HPPs on riverine ecosystems is particularly pronounced in periods of moderate flows, when minimum water flow prescribed by the law does not discharge into the river (Wu et al. 2010; Fijko et al. 2017). Wu et al. (2010) researched and proved the significant effects of small HPPs on the benthic algal community in terms of different physical and chemical conditions between control and dammed sites, a significant increase in chlorophyll-a concentration, total algal density and major impact on the overall benthic algal community in dry periods.

Perhaps the most striking negative ecological impact of small HPPs is observed at the multiple installation level. The presence of multiple installations reduces conductivity in rivers and impedes the dispersal ability of freshwater organisms (Kibler & Tullos 2013). The cumulative effects of small HPPs are observed on the Vlasina River, where nine small HPPs are already constructed and several are planned for construction (Ministry of Mining and Energy of Republic of Serbia). During our field surveys, the watercourse downstream from the constructed small HPPs was devasted and no benthic algae were observed.

Since *Lemanea* species were found at only 14 locations in Serbian riverine ecosystems affected by the above-mentioned threat factors, their protection and protection of their habitats is necessary. The construction of HPPs, especially small HPPs, planned in pristine upland-mountain Serbian rivers will destroy most of the *Lemanea* habitats along with the habitats of strictly protected Rhodophyta species.

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