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The Aquatic Plant Communities of Lake Murten

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Abstract

In Switzerland, there are hardly any current scientific publications on aquatic plant communities. There are also very few studies of the flora and vegetation of Lake Murten. In 2019 during a single vegetation period, the vegetation conditions in Lake Murten were recorded using boat and dive mapping. In the process, 10 associations consisting of three plant alliances were detected and documented using phytosociological surveys. The five most common aquatic plant communities are *Potametum pectinati* Carstensen ex Hilbig 1971, *Myriophylleto-Nupharetum* Koch ex Hueck 1931, *Phragmitetum australis* Soó 1927 nom. mut. Balátová-Tulácková et al. 1993, *Potametum lucentis* Hueck 1931, and the *Schoenoplectetum lacustris* Eggler 1933. The vegetation boundary in the lake has doubled compared to 1979, from 3,0 m to 6,0 m due to reduced nutrient inputs. The studies in Lake Murten make a regional contribution to the knowledge of native aquatic plant communities.

Keywords : depth distribution, macrophytes, phytosociology, vegetation change.

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Zusammenfassung

In der Schweiz gibt es kaum aktuelle wissenschaftliche Veröffentlichungen über Wasserpflanzengesellschaften. Auch vom Murtensee gibt es nur sehr wenige Untersuchungen zur Flora und Vegetation. 2019 wurden innerhalb einer Vegetationsperiode die Bewuchsverhältnisse im Murtensee durch Boots- und Tauchkartierungen erfasst. Dabei wurden 10 Assoziationen aus drei Verbänden nachgewiesen und mit pflanzensoziologischen Aufnahmen belegt. Die fünf häufigsten Wasserpflanzengesellschaften sind das *Potametum pectinati* Carstensen ex Hilbig 1971, das *Myriophylleto-Nupharetum* Koch ex Hueck 1931, das *Phragmitetum australis* Soó 1927 nom. mut. Balátová-Tulácková et al. 1993, das *Potametum lucentis* Hueck 1931 und das *Schoenoplectetum lacustris* Eggler 1933. Die Vegetationsgrenze im See hat sich, im Vergleich zu 1979, aufgrund verringerter Nährstoffeinträge von 3,0 m auf 6,0 Meter verdoppelt. Die Untersuchungen im Murtensee leisten einen regionalen Beitrag zur Kenntnis der heimischen Wasserpflanzengesellschaften.

Schlüsselwörter : Makrophyten, Murtensee, Phytosoziologie, Vegetationsveränderung, Tiefenverbreitung, Wasserpflanzengesellschaften.

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Introduction

Plant communities are regular, typable associations of plants, each of which is distinguished from other types of vegetation by the presence of certain species (Dierschke 1994 ; Wilmanns 1984). The science of plant associations is usually referred to as vegetation science, phytocenology, or plant sociology.

Currently, however, the aquatic plant communities in Switzerland lead a shadowy existence. The author is unaware of any recent (not older than ten years) publications dealing with the distribution and composition of aquatic plant communities (at the association level) in Switzerland.

Vegetation studies are available from countries bordering Switzerland, but most are also ten years old or older. In Franche Compté (F), some phytosociological work has been done on aquatic plants. Bailly *et al.* (2007) provided a comprehensive work on aquatic plant communities in ten lakes of the Jurassic Massif, but without publishing the associated vegetation records. Bardat *et al.* (2013) published the "Prodrome des végétations de France", wherein all vegetation units of the French flora are listed on 143 pages at the association level.

Pott (1995), in his overview of plant communities in Germany, also deals with vegetation in aquatic habitats. However, it is only in 2002 that a complete list of all plant communities known in Germany was presented (Rennwald 2002). The formation of aquatic plant communities is treated on twelve pages. This list is on the association level, but without the important phytosociological tables and location information. Only the exemplary and very detailed work of Bettinger & Wolff (2002) treats the vegetation of a whole federal state (Saarland) in detail within a series of atlases. In volume II, the aquatic plant communities are treated in detail at association level over 97 pages, including the presentation of the phytosociological tables in both a text and digital appendix. The distribution of the communities is comprehensibly documented.

In Mucina *et al.* (1993), all associations and higher syntaxa ever known or described in Austria are described based on primary and secondary literature, including "grey literature" (e.g. diploma theses, dissertations, field trip reports). Volume II incorporates a 79-page record of the aquatic plant communities at the association level. There are no association tables and, also distribution maps are absent.

Various works on aquatic plant communities are also known from other European countries, e.g., Weekes *et al.* (2018) for aquatic plant communities in the streams of Ireland, Jablonska & Klosowski (2012) for characeous communities in the still waters of Poland or Zervas *et al.* (2020) for lakes in Greece.

Ecological work on individual aquatic plant species in Switzerland and population analyses are available (e.g., Auderset Joye & Boissezon 2017, Boissezon *et al.* 2017). However, no phytosociological communities or phytosociological community distribution have been studied in Switzerland. In the past decades, there have been some comprehensive scientific works and surveys on aquatic plants in Swiss lakes, e.g., by Lehmann & Lachavanne (1999), by the Office for Water and Waste Bern (Guthruf *et al.* 2015) or by the Lake Lucerne Supervisory Commission (AquaPlus 2012). However, these were, without exception, papers on floristics or autecology, where the patterns of association of the species and their importance were not addressed.

An overview of the plant communities occurring in Switzerland is provided by the compilation "PhytoSuisse" at Infoflora (Prunier *et al.* 2019). This was created a few years ago under the aegis of the Vegetation Helvetica Commission as a summary of the available literature. The

objectives of Vegetation Helvetica include the further development of vegetation studies using phytosociological methods, their teaching and application, and scientific exchange at national and international levels. The current main activity is the complete processing of the plant communities of Switzerland. Currently, 81 aquatic plant communities are listed for Switzerland in the publicly accessible database Info Flora. Of these, 20 communities belong to the *Charetea*; 61 belong to the classes (*Lemnetea*, *Littorelletea*, *Potametea* and *Utricularietea*).

Aware of the lack of current data, the studies in Lake Murten make a regional contribution to the knowledge of native aquatic plant communities.

Methods

Various techniques were used to record the vegetation conditions in Lake Murten completely and uniformly within one growing season in 2019. A uniform survey of the entire littoral was conducted using a kayak (figure 1). The survey of emersed and submerged vegetation was ensured by good visibility conditions. A telescopic rake or a grappling hook (figure 2) was used to determine vegetation limits, when vegetation conditions were unclear, or when plant material was removed. Conductivity and water temperature measurements were made with a Multi-Parameter Portable Meter (WTW ProfiLine pH/Cond 3320). The same applies to measurements of the pH value (measured with a SenTix 41 pH electrode, WTW).

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Figures 1-4. 1. Kayak with material for investigation. **2.** Grapnel. **3.** Secchi-disk. **4.** Scuba-diver during investigation. Photos: A. Schwarzer.

The depth of visibility was determined with the aid of a Secchi disk (HYDRO-BIOS). For this purpose, the white perforated disc was slowly lowered into the water on a string until it was no longer visible (figure 3). Since the depth of visibility correlates well with algal density and thus with phosphorus concentration in most lakes (excluding those with mineral-induced turbidity), it not only provides information about the colonisation depths for macrophytes, but it also allows to evaluate the intensity of primary production (trophic level) (Carlson 1977). To improve reproducibility, measurements were, as far as possible, taken at the same time (i. e., between 10:30-13:30).

However, diving surveys were essential for the semi-quantitative determination of macrophyte colonisation along a depth gradient, documentation of the absolute limit of colonisation, and targeted follow-up searches for specific species (figure 4).

For the phytosociological survey of aquatic plants, abundance ratios were estimated following Braun-Blanquet's seven-part abundance-dominance scale:

r: only 1 individual present in the recording area
+: sparse, covering only a small area (< 5%)
1: numerous, but < 5 % covering or sparse, but with larger covering value
2: 5-25 % opaque or very numerous individuals but less than 5 % opaque
3: 25-50 % of the surface covering
4: 50-75 % of the surface opaque
5: covering more than 75 % of the surface

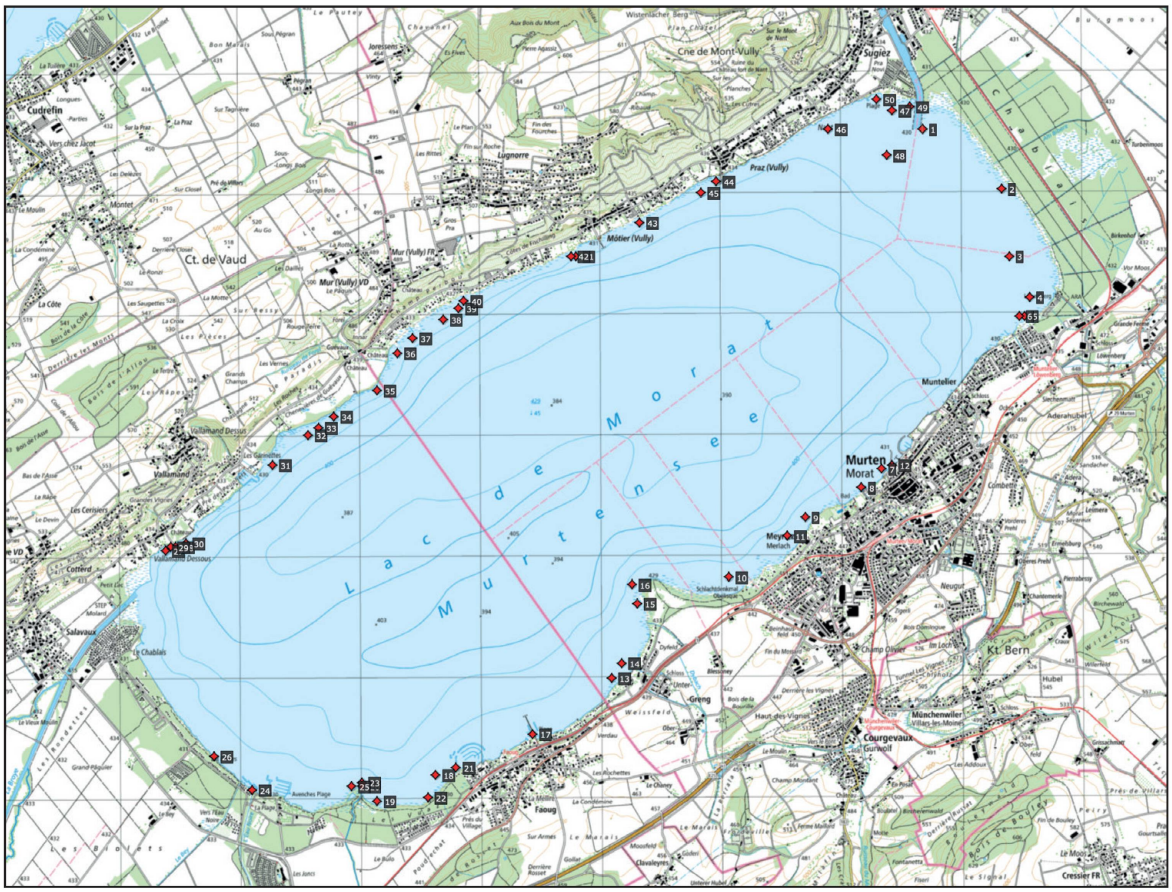

Figure 5. Overview of the location of the surveys in Lake Murten. Map basis: map.geo.admin.ch

The exact location of the phytosociological surveys was recorded by GPS. Samples were taken from systematically critical species (especially genus *Potamogeton*, *Characeae*) and re-determined. Particularly remarkable finds were documented photographically or preserved as alcohol samples.

Results

Plant sociological recordings and associations

Fifty phytosociological surveys were conducted in Lake Murten, distributed throughout the lake littoral (figure 5). The geographical coordinates of the recordings and the associated associations are listed in Appendix 1.

A total of 23 aquatic plants were recorded, distributed among ten communities. The nomenclature and systematics refer to Prunier *et al.* (2019)(table 1).

Table 1. Overview of the aquatic plant communities of Lake Murten.

Alliance	***Charion vulgaris* Krause et Lang ex Krause 1981**	
Associations	1. *Nitellopsidetum obtusae* Dambska 1961	2 surveys
	2. *Charetum contrariae* Corillion 1957	3 surveys
Alliance	***Potamion pectinati* Koch ex Görs in Oberd. 1977**	
Associations	3. *Potametum lucentis* Hueck 1931	8 surveys
	4. *Potametum perfoliati* Miljan 1933	3 surveys
	5. *Potametum pectinati* Carstensen ex Hilbig 1971	11 surveys
	6. *Najadetum marinae* Libbert 1932 ex Fukarek 1961	4 surveys
Alliance	***Nymphaeion albae* Oberd. 1957**	
Association	7. *Myriophylleto-Nupharetum* Koch ex Hueck 1931	9 surveys
Alliance	***Parvopotamion* Vollmar 1947**	
Association	8. *Ceratophylletum demersi* Corillion 1957	2 surveys
Alliance	***Phragmition australis* Koch 1926 *nom. mut. prop.* Bardat et al. 2004**	
Associations	9. *Schoenoplectetum lacustris* Eggler 1933	5 surveys
	10. *Phragmitetum australis* Soó 1927 nom. mut. Balátová-Tulácková et al. 1993	3 surveys

Distribution and abundance of aquatic plant communities in the lake

The classification of the aquatic plant communities of Lake Murten is based on the overriding principle of dominance since the aquatic associations – compared to terrestrial communities – are rather species-poor. Associated species indicate the site-specific features within an association.

Widespread associations

The table of aquatic plant communities (table 2) does not reflect the abundance ratios of the individual communities in the lake. The characeous communities are underrepresented; the same is true for the reed communities. The most widespread are the following five associations:

***Potametum pectinati* Carstensen ex Hilbig 1971 (columns 6-16)**

This community is by far the most abundant in Lake Murten. It is particularly strong in the shallow littoral zones between the Broye Canal and Muntelier in the northeast, Avenches Plage and Le Chablais Plage in the southwest, and below the mouth of the River Broye to Vallamand (figures 6-7). Despite its abundance, it is hardly noticeable due to its submersed growth. However, under the water surface, it can form very dense populations. Its predominant depth distribution is between 1.2-2.5 m. The community benefits, on the one hand, from the nutrient inputs of the Broye river and, on the other hand, from external disturbance created by recreational use (bathing and boating).

Potamogeton berchtoldii and *Ranunculus circinatus* often co-occur in dense populations. In contrast, *Characeae* or *Najas marina* are found more frequently in less dense populations, in both shallow and deep waters.

***Myriophylleto-Nupharetum* Koch ex Hueck 1931 (columns 34-42).**

This association forms a dominant community in many places in Lake Murten. It is optimal occurrence is at depths between 1-3 m and can occupy contiguous areas of well over 1 000 square meters. The community can form dense populations in sheltered places such as shallow bays or behind offshore *Schoenoplectus lacustris* reeds, where only marginal companion species such as *Characeae* or *Najas marina* occur (figures 8-9).

In wind-exposed places, especially the shore zones exposed to westerly winds between Faoug and Muntelier, we find *Myriophylleto nupharetum* often growing in small areas and with transitions to *Potametum lucentis* and *Schoenoplectetum lacustris*. Since wave action can destroy the emersed leaves, the plant grows submerged even in shallow water. The character species *Nuphar lutea* is limited in its depth distribution. The stems of the emersed leaves reach a maximum length of 4 m.

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Figures 6-7. 6. *Potametum pectinati* in deeper water at Vallamand, near the mouth of the Broye. **7.** In shallow water, east of the Broye Canal near Sugiez. Photos: A. Schwarzer.

***Phragmitetum australis* Soó 1927 nom. mut. Balátová-Tulácková et al. 1993 (columns 48-50).** The reed is the dominant species of the reed zone in Lake Murten. As a typical riparian species, it can penetrate onshore and grow offshore to depths of 2 m. The species is present in all shore areas of Lake Murten. Large occurrences are found in the sections between Sugiez and Mutelier, Meyrier and Faoug, and Guiveau and Nant (figures 10-11).

The character species *Phragmites australis* possesses partially woody and bend-resistant stems, which makes it good at absorbing wave and wind action to a certain degree; this resilience is further enhanced because the plant does not form underwater leaves. As soon as the stalks buckle, the plant dies. The reed does not tolerate strong water level fluctuations. The species reproduces mainly vegetatively via stolons. Its dense, deep rhizome network prevents the emergence of other helophytes and macrophytes. The densest populations are found in shallow water at depths up to 1 m. These are often single species populations. However, low density (i. e., few plants per square metre) populations with either *Characeae* undergrowth or various *Potamogeton* species go much deeper. In places with strong wind and current, the reed is replaced by *Schoenoplectetum lacustris*.

Figures 8-11. 8. Dense *Myriophylleto-Nupharetum* on the northeast shore of the lake, developed as a closed band in front of the *Phragmitetum australis*. **9.** *Myriophylleto-Nupharetum* with gaps, with submerged leaves of *Schoenolectus lacustris* on the south-east lakeside. **10.** *Phragmitetum australis* with gaps, exposed to strong winds. The turbidity is also caused by the strong winds. Litoral zone west of Faoug. **11.** The protective *Phalaris*-belts are often disrupted by private use. Between Château Guevaux and the public jetty in Motier, on a shore length of only 2 km, there are 48 jetties that cut through the reeds. Photos: A. Schwarzer.

Table 2. Matrix of the Aquatic Plant Communities of Lake Murten.

Characterspecies of the association
Charetum contrariae Corillion 1957
Charetum contrariae Corillion 1957
Potametum pectinati Carstensen ex Hilbig 1971
Potametum perfoliati Miljan 1933
Potametum lucentis Hueck 1931
Najadetum marinae Libbert 1932 ex Fukarek 1961
Ceratophylletum demersi Corillion 1957

Column	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Survey No	4	3	5	3	6	1	1	2	3	6	1	5	3	2	2	3	7	1	3	3	1	2	4
Water depth/ m	1,8	1,8	1,1	4,1	1,5	1.2	1,2	1,3	1,2	2,5	1,3	2	3,5	1,3	1,5	1,4	3	3,5	4,5	2	1,6	2,5	3,5
Substrae	sandy gravel	sandy mud	sand	sandy mud	mud	gritty sand	gritty sand	sand	sand	gritty mud	muddy gravel	muddy sand	mud	sand	sand	sand	gritty sand	sandy mud	mud	sandy gravel	sand	sand	sand
Area qm	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20
Number of species	5	8	6	7	6	4	6	8	7	6	10	7	6	5	7	5	8	7	9	4	8	5	5
Total cover %	90	95	65	95	100	90	90	85	85	80	100	80	80	80	50	40	70	75	75	100	80	85	70

Species

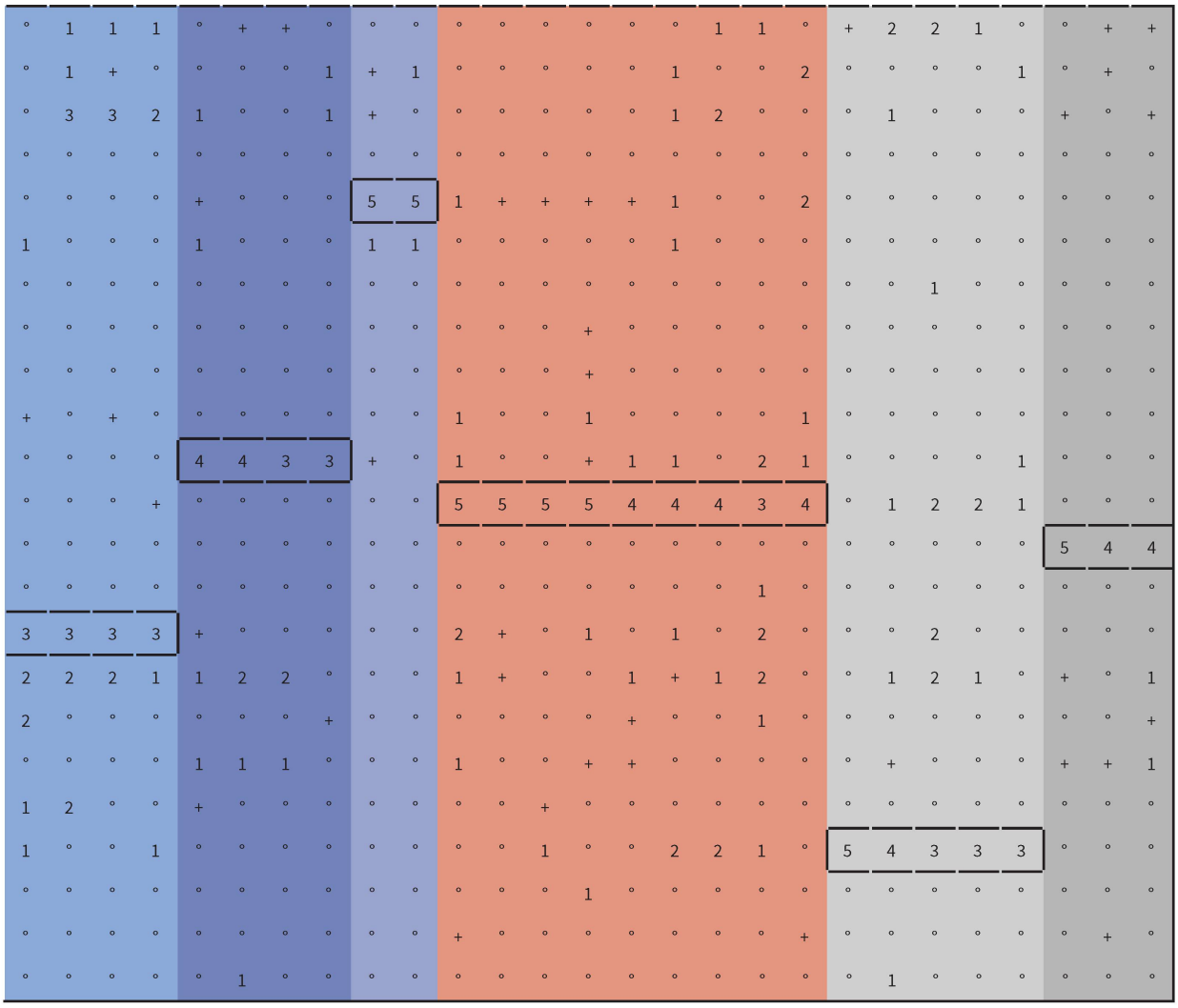
Chara contraria	3	3	3	°	+	3	3	3	2	2	1	1	°	1	+	+	°	1	1	°	1	°	°
Chara globularis	2	2	1	1	+	1	1	+	1	1	1	2	2	°	°	°	°	°	1	°	+	°	1
Nitellopsis obtusa	3	1	1	4	5	2	2	2	1	1	2	1	°	°	+	+	°	+	2	°	°	°	°
Nitella opaca	°	°	°	°	+	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°
Ceratophyllum demersum	°	°	°	°	°	°	°	°	°	°	°	°	°	+	°	°	°	°	°	°	°	°	°
Elodea nuttallii	°	°	°	1	°	°	°	°	°	°	1	°	1	°	°	°	°	°	°	°	°	°	°
Fontinalis antypyretica	°	°	°	°	°	°	°	°	°	°	°	1	°	°	°	°	°	°	°	1	1	°	°
Lemna minor	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°
Lemna trisulca	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°
Myriophyllum spicatum	+	+	°	+	°	°	°	°	+	°	°	°	°	°	+	°	+	°	°	°	°	°	°
Najas marina	°	+	°	1	°	°	+	1	°	°	1	1	2	2	°	+	°	+	1	°	1	1	°
Nuphar lutea	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	1	1	+	+	1	1	2
Phragmites australis	°	°	°	°	°	°	°	°	+	°	°	°	°	°	°	°	°	°	°	°	°	°	°
Potamogeton crispus	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°
Potamogeton lucens	°	°	1	2	°	°	°	+	°	°	1	°	°	°	°	°	2	2	2	5	4	4	3
Potamogeton pectinatus	°	2	3	2	+	4	4	4	4	4	4	4	4	4	3	3	1	°	2	°	°	1	1
Potamogeton perfoliatus	°	°	°	°	°	°	°	°	°	°	+	°	°	°	+	+	3	3	3	+	1	1	°
Potamogeton bercholdii	°	1	°	°	+	°	1	1	°	1	2	1	1	°	1	°	+	°	+	°	°	°	°
Ranunculus circinatus	°	°	°	°	°	°	°	°	°	2	1	°	2	°	°	°	+	°	°	°	°	°	°
Schoenoplectus lacustris	1	°	1	°	°	°	°	°	+	°	°	°	°	1	+	°	1	+	°	°	1	°	2
Spirodela polyrhiza	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°
Utricularia australis	°	°	°	°	°	°	°	1	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°
Zannichelia palustris	°	+	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°

Myriophylleto-Nupharetum Koch ex Hueck 1931

Schoenoplectetum lacustris Eggler 1933

Phragmitetum australis Soó 1927 nom. mut. Balátová-Tulácková et al. 1993

24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
4	2	5	2	2	3	5	5	5	4	1	2	3	1	3	1	1	1	2	4	4	1	3	2	2	6	4
1,8	2,1	3,5	2	1,6	1,3	1,2	4,1	4,5	5	1,6	1,1	1,4	1,1	1,3	2	1,5	4	1,5	2,2	1,4	2,1	2,1	1,2	0,8	0,8	0,8
gritty sand	mud	gritty sand	chalkmud	muddy gravel	clay	schlam. Sand	sandy mud	mud	mud	mud	sand	gritty sand	sandy mud	gritty mud	mud	muddy gravel	sandy mud	sandy mud	sand	sand	gritty sand	gritty sand	sand	sand	sand	sand
20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20
7	6	5	6	8	5	4	4	5	3	8	4	4	9	6	9	5	8	6	1	7	6	4	4	4	5	6
70	100	75	70	100	90	70	60	90	100	100	90	90	80	100	100	90	80	95	100	85	70	50	50	95	70	75



***Potametum lucentis* Hueck 1931 (columns 20-27)**

Potamogeton lucens is a large-leaved, submerged pondweed that occurs in both still waters and strongly flowing streams due to its robust habitus. The plant is meso- to eutrophic, but sensitive to pollution and phosphate inputs. The species is one of those spawning weeds that penetrate deepest into the littoral and can still grow at depths of 7-8 m, provided the light penetration depth is sufficient for the species to grow.

Potametum lucentis occurs everywhere in Lake Murten and, along with *Potametum pectinati*, is one of the most frequent and widespread associations quantitatively. The densest occurrences are in the southwestern area of Lake Murten, between Grengspitz and Guéveaux, and between Löwenberg and Murten in the northeastern lake area (figures 12-13).

***Schoenoplectetum lacustris* Eggler 1933 (column 43-47)**

The *Schoenoplectus lacustris* is a siltation pioneer in the shore zones of meso- to eutrophic waters. Of all reed species, it can penetrate farthest into the water, often forming only ribbon-like underwater leaves at depth. In contrast to the reed, *Schoenoplectus lacustris* is less competitive on land, but more competitive on water. The round, bend-resistant stems also assimilate

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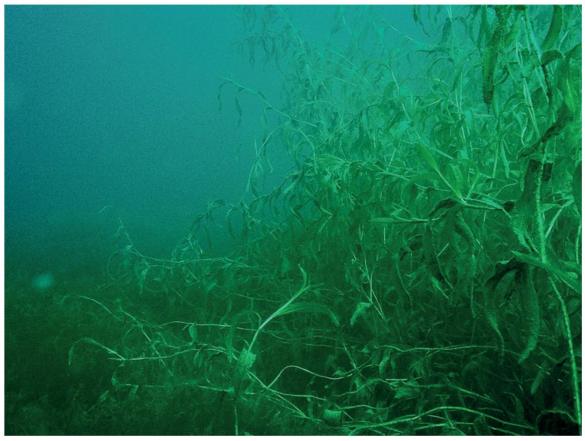

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Figures 12-15. 12. The *Potamteum lucentis* occurs both in shallow water and near the macrophyte depth limit in Lake Murten. In shallow water, this community is often closely intertwined with the reed communities. **13.** In particular, between Avenches Plage and Le Chablais, this community is not found in shallow water, but regularly between 4-5 m depth, together with the submerged *Nuphar lutea* and *Potamogeton perfoliatus*. **14.** Dense *Schoenoplectetum lacustris*, which is growing in front of the *Phragmitetum australis*, in the littoral zone between Mur and Praz. **15.** Stand of *Schoenoplectus lacustris*, with submerged, ribbon-shaped leaves. Photos : A. Schwarzer.

underwater and tolerate current and wave action well. The species copes better with water level fluctuations than the reed, but less well with desiccation.

Schoenoplectus lacustris is the most common macrophyte in Lake Murten, along with *Potamogeton lucens* and *P. pectinatus*. The species forms large, dense, and extensive stands located in front of the reeds and often extend into the floating or submerged leaf zone. It can be found in all sections of the shore and especially frequently in the shore sections on the north and south shore.

Schoenoplectetum lacustris forms dominant community in Lake Murten. Depending on the disturbance intensity (e.g., at bathing sites) and water depth, this is interspersed with pondweed species in varying proportions. Emersed occurrences of this species in Lake Murten reach a depth of 3.2 m, and submerged occurrences down to a depth of 4 m (figures 14-15).

Less frequent associations

Significantly rarer in Lake Murten is ***Najadetum mariane*** (columns 28-31). The association species, *Najas marina*, is a thermophilic therophyte that develops anew annually only in summer from overwintering seeds. The species is restricted to waters that warm strongly in summer. Contrary to references in the literature, *Najas marina* occurs in native waters not only in shallow water (0.5-1.5 m) but also in deeper zones. The community can spread strongly under favourable conditions and overgrow other aquatic plant populations.

Particularly dense populations are found in shallow water near Faoug, Vallamand and between Guevaux and Vully. In Lake Murten, however, the species also occurs in deeper areas still colonised by macrophytes. It invades the *Potametum pectinati* and the *Potametum lucentis* and is also regularly found in the *Myriophylleto-Nupharetum*. Not infrequently in Lake Murten, *Najas marina* forms the vegetation boundary at 5 m depth (figures 16-17).

The characterising species of the ***Nitellopsidetum obtusae*** (column 4-5), *Nitellopsis obtusa*, occurs in all large lakes of Switzerland. Large populations are now known on Lake Biel, Lake Zurich, and Lake Lucerne. The species was first recorded in Switzerland at the beginning of the 20th century, and since then, its range has continuously increased. Formerly known only

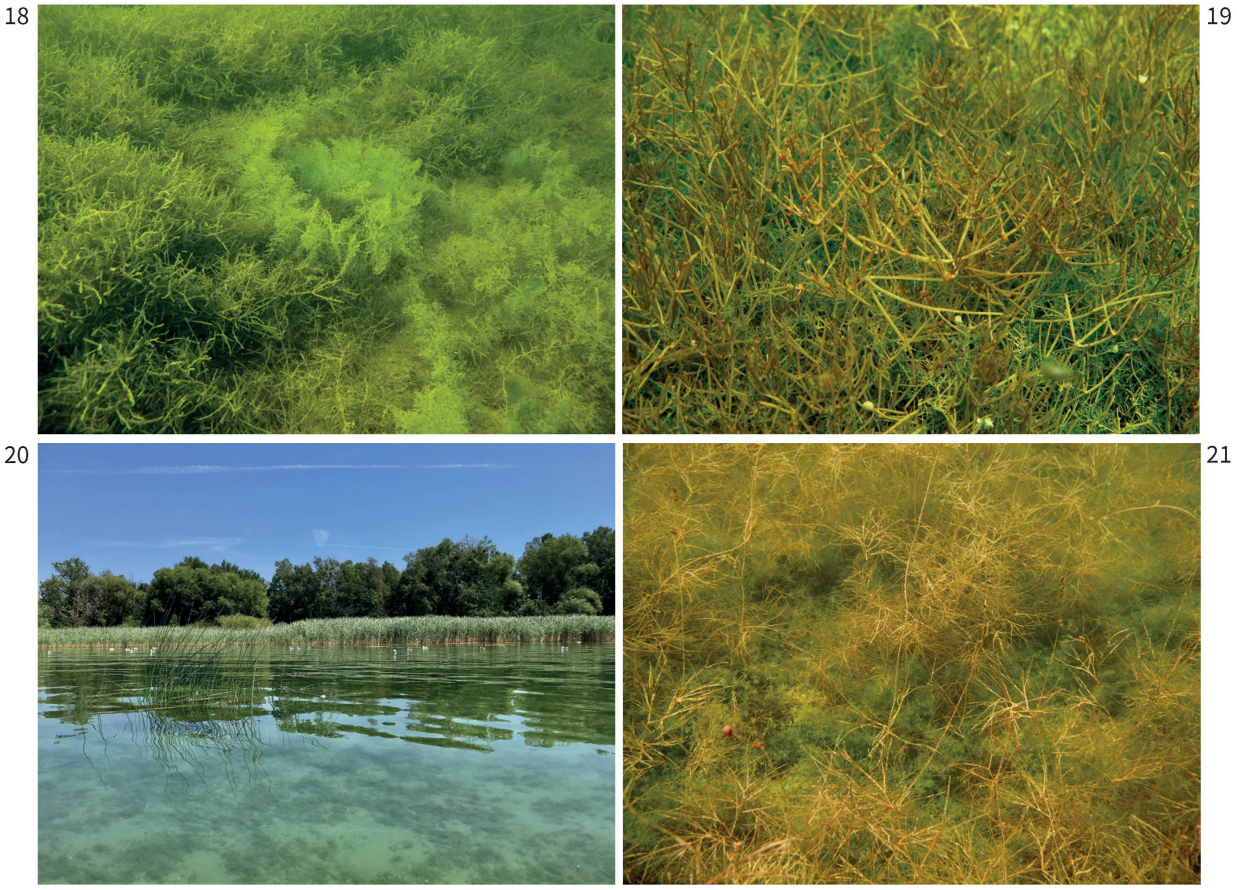
16 17

Figures 16-17. 16. *Najadetum marinae*, community formation with many *Characeae* and *Schoenoplectus lacustris*, f. *submersa*. Near Môtier, 4 m depth. **17.** *Najas marina*, shoot and leaves in size comparison with a *Nuphar lutea* leaf. Photos: A. Schwarzer.

in the deep water of oligotrophic lakes, it has changed location. It can now also be found in Switzerland in shallow water near the shore. Until a few years ago, *N. obtusa* was not known in Lake Murten. It was first recorded in 2011 (Sesa 2012). The species is usually annual and dies in late summer/early fall. However, it can also persist green in deep water. *Nitellopsis obtusa* is rarely fertile, usually growing from overwintering bulbils. However, fertile specimens were frequently observed in Lake Murten during the 2019 study period.

Surprisingly, the aerial survey of Lake Murten shows that *Nitellopsidetum obtusae* occurs everywhere in the lake littoral, but in very different abundances. It is most abundant in the littoral areas between Löwenberg and Murten, between Salavaux Plage and Vallamand, and between Praz and Sugiez, where it occurs mainly in shallow water and penetrates the *Potametum pectinati*. However, in many locations on the lake, the community is also found at depths up to near the vegetation limit between 4-5 m depth. Quantitatively, *Nitellopsidetum obtusae* is currently Lake Murten's most common characeous community (figures 18-19).

Charetum contrariae (columns 1-3) is present in all shore areas of Lake Murten but is nowhere frequent or plentiful. However, the association is found in practically all shallow water sites, although often only fragmentarily, and is also regularly found in the undergrowth



Figures 18-21. 18. *Nitellopsidetum obtusae*, with submerged leaves of *Utricularia vulgaris*. Diving transects near Murten, 2.5 m depth. **19.** Dense *Nitellopsidetum obtusae*, fertile individuals with red colored gametangia. Diving transects near Murten, 2.5 m depth. **20.** *Charetum contrariae* with a lot of gaps, in the extensive shallow water of the littoral between the Broye Channel and Löwenberg. **21.** Dense *Charetum contrariae* with *Potamogeton pectinatus*, in shallow water between Nant and Broye Channel. Photos: A. Schwarzer.

of *Potamogeton* populations. In the dense floating-leaf communities dominated by the Great Pond Lily (*Nuphar lutea*), it is represented only marginally, if at all, due to the heavy shade.

In Lake Murten, the presence of *Charetum contraria* is distinctly focused on the shallow littoral, i. e., in the area between reed and pondweed communities. In deeper areas, it is practically absent because of unfavourable light conditions (figures 20-21).

Ceratophylletum demersi (column 32-33) is not common in Lake Murten. As a drifted single plant, the species is mostly found in shallower water, and mainly in the littoral between Faoug and Avenches Plage. It is only found in large amount between Vallamand and Mur. The nutrient-rich waters of River Broye and River Petite Glâne probably contribute to the large occurrence of this community in this location, where it can occur up to 5 m depth.

C. demersum overwinters as a shoot on lakebed and only floats to the surface when the water warms up considerably. The species reproduces in Switzerland mainly vegetatively by torn-off shoot pieces or side shoots. It lives completely submerged as a free-swimming plant or only slightly anchored by rhizoids in soft mud. It is very shade tolerant and occurs in "dark" waters that no other submerged species can penetrate. It can form meter-long shoots that grow together to form dense, impenetrable forests (figures 22-23).

Potametum perfoliati (columns 17-19) is much rarer in Lake Murten than *Potametum lucentis* or *Potametum pectinati*.

Single plants can be found almost everywhere, but the species rarely forms a community. *Potametum perfoliati* is most frequently found in shallow water between Praz and Vully, interspersed between the *Charetum contrariae* and the *Potametum pectinati*, or in deeper areas near Avenches Plage or Vallmand.

Potamogeton perfoliatus and *P. lucens* form the most extended shoots among aquatic plants and are found in clear lakes down to 7 m deep. This meso- to eutrophic species is found in lakes, ponds, oxbow lakes, and rivers. The plant tolerates strong currents and wave action and is often found around boat docks in native lakes. It grows on stony gravelly substrates as well as on muddy bottoms (figures 24-25).

22

23

Figures 22-23. 22. *Ceratophylletum demersi* at 5 m depth. The plants cover the entire substratum. Diving transects near Murten. **23.** *Ceratophyllum dermersum*, single plant, in a dense stand of *Nitellopsis obutsa* and *Najas marina*. Photos: A. Schwarzer.

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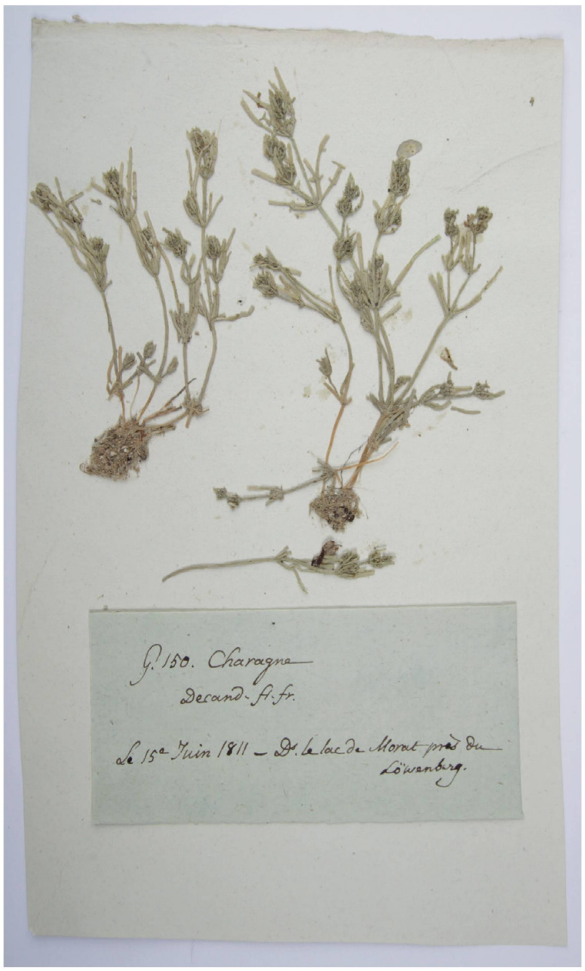
Figures 24-25. 24. *Potametum perfoliati* in Lake Murten often occurs almost up to the vegetation line, or together with *P. lucens* forms dense underwater forests between 3 to 4.5 m depth. **25.** Growth form of a solitary *Potamogeton perfoliatus* plant in shallow water. Photos: A. Schwarzer.

26



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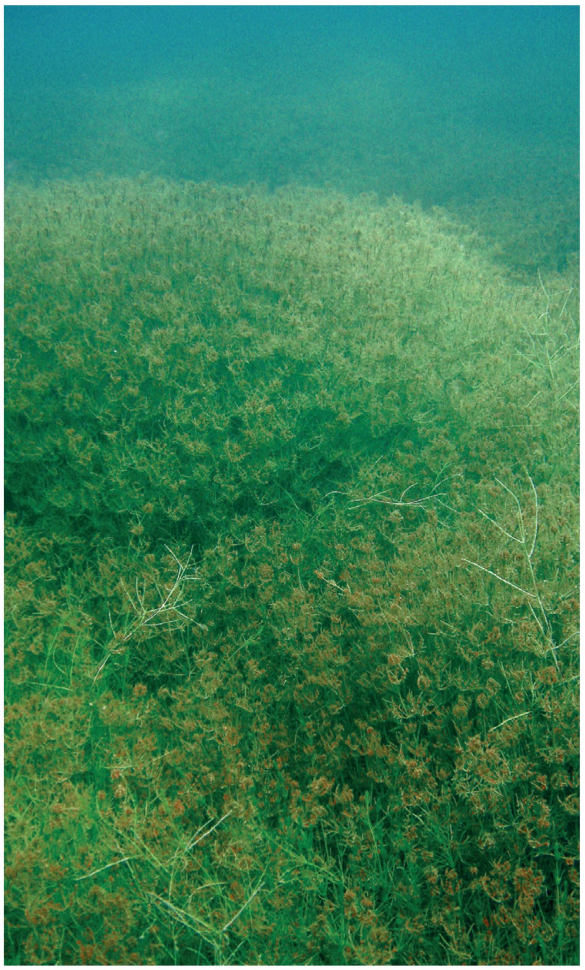

Figures 26-27. 26. Specimen of Coral Stonewort (*Chara tomentosa*) from Lake Murten, found in the Herbarium at the Natural history Museum Fribourg (NHMF). **27.** Dense *Magnocharetum tomentosae* Corillion 1957 from Lake Lucerne. The community occurs predominantly in nutrient-poor large lakes and forms either dense single-species stands in shallow water or dominant stands together with *Chara globularis*, *C. hispida*, *C. contraria*, *C. filiformis*, as well as *Potamogeton pectinatus* and *P. friesii*. Photos: A. Schwarzer.

Discussion

Changes in vegetation - Historical records and previous aquatic plant surveys

In the Herbarium at the Natural history Museum Fribourg (NHMF) there is a record of *Chara tomentosa* being found in Lake Murten (figures 26). The Coral Stonewort was collected at Löwenberg in 1811. Since that date, the species has not been recorded in Lake Murten.

The record probably comes from Claude Gay, a Swiss botanist who was active in this region and collected *Characeae*. Braun (1847) quotes him in his overview of the Swiss *Characeae*. *Chara tomentosa* is mentioned again in connection with Lake Murten by Krause (1997), but without dates. It needs to be listed in the Info Flora for Lake Murten.

Based on the sparse information, it is difficult to assess whether *Chara tomentosa* was rare or abundant in Lake Murten.

The main cause of the decline and extinction of this characean species in Lake Murten is probably the eutrophication of the lake, which has been decreasing continuously since the 1980s. The main factor here is the total phosphorus concentration. From the beginning of the new millennium, the total phosphorus content in the lake has stabilized increasingly frequently at a mesotrophic level, permanently falling below the 30 mg/m^3 value critical for many *Characeae* (https://www.die3seen.ch/site/wp-content/files/2009/02/Phosphor-1982-20.pdf).

Figure 28 shows the visibility depth in Lake Murten over the year. During the vegetation period, the measured values are in a range typical for mesotrophic lakes (figure 29). However,

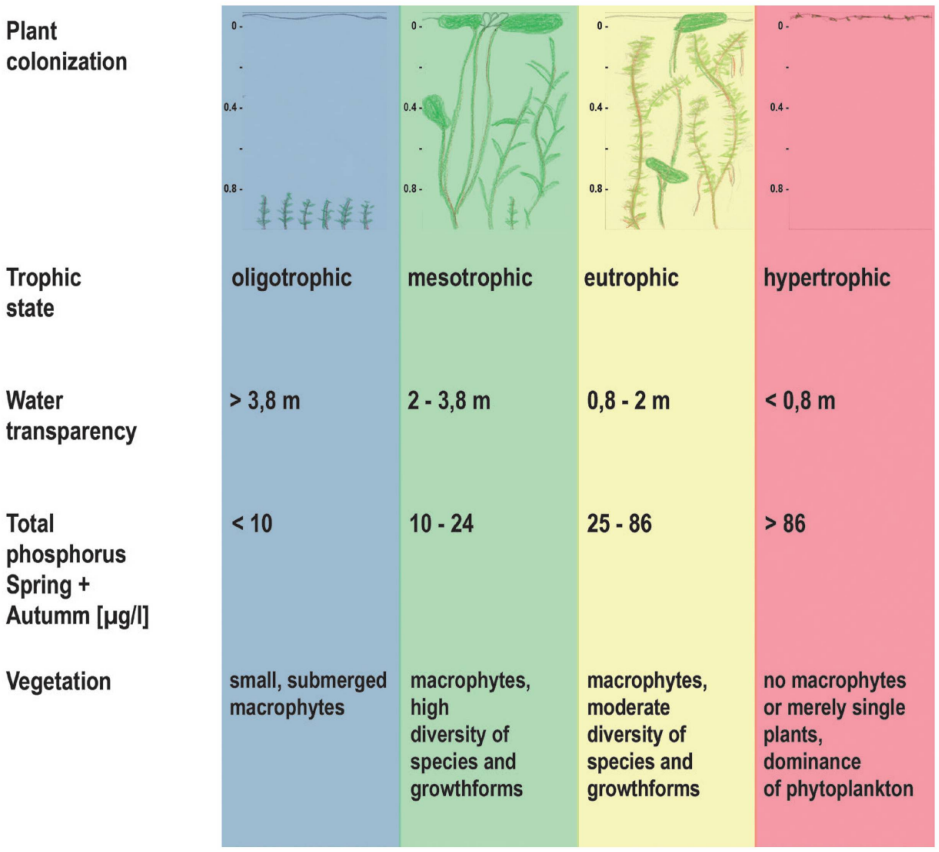

Figure 28. Correlation between macrophyte colonization, trophic state, water transparency and total phosphorus content in open water. After LAWA (1998), modified and supplemented.

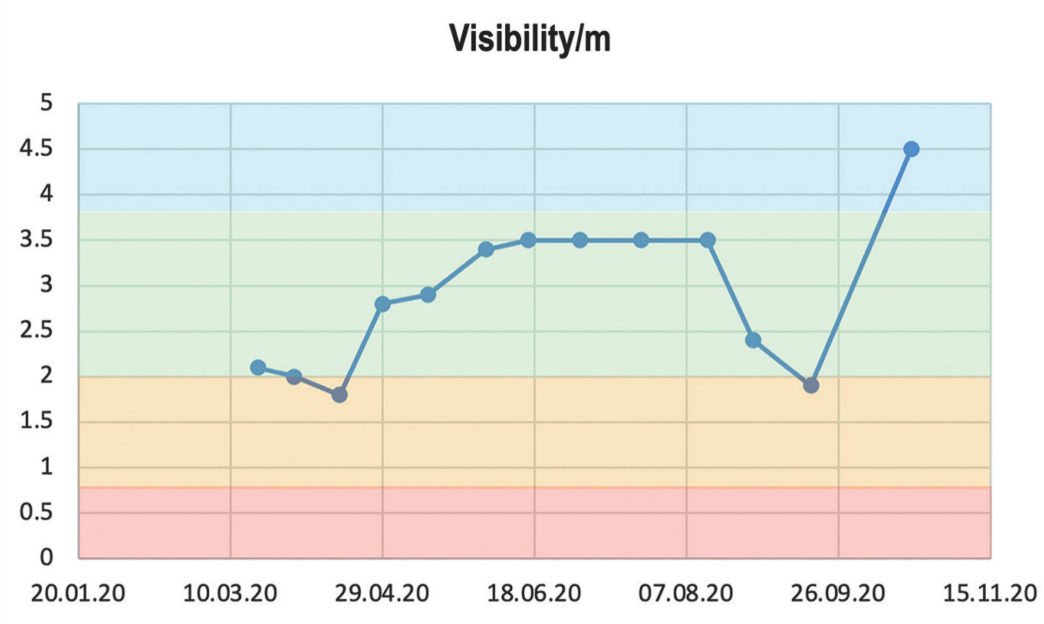

Figure 29. Visibility measurements at the Vallamand jetty, between March and October 2020. Visibility is a good measure of the trophic status of the lake. Sufficiently frequent measurements during the vegetation period therefore give a good indication of the trophic status.

for light-demanding characeous communities, such as the *Magnocharetum tomentosae*, the *Charetum filifomis* or the *Charetum asperae*, the water of Lake Murten is still too turbid and nutrient-rich. However, mesotrophic communities such as the *Nitellopsitdetum obtusae* and the *Charetum contrariae* can already cope with these growing conditions.

Compared to other lakes, Lake Murten has been little studied in terms of its flora and vegetation. The first systematic surveys were carried out by Lachavanne (1979) and later by Sesa (2012). Since then, further surveys have yet to be conducted. However, the reference in Lachavanne is significant to the depth of colonisation of aquatic plants in the lake, which he still gives as 3 m. This has changed significantly over the last 40 years.

Mainly, the plant communities extend as bands through specific depth ranges. *Ceratophylletum demersi*, or *Najadetum marinae*, is currently found in the deepest places. The vegetation boundary usually does not end abruptly, but the population thins slowly until only individual plants remain (table 3 ; figures 30-31).

Table 3. Distribution depth of selected species and absolute limit of colonisation in Lake Murten, 2020.

Species	Depth (m)
Ceratophyllum demersum	6.0
Nuphar lutea (f. submersa)	4.5
Najas marina	5.1
Schoenoplectus lacustris (f. submersa)	4.0

30   31

Figures 30-31. 30. Abrupt vegetation limit in Lake Murten, at 4.5 m depth. Single *Nuphar lutea* plant in front of a dense band of *Najas marina*. **31.** Low growing *Najas marina* single plant at 6.0 m depth. Photos: A. Schwarzer.

Study limitations

The fifty phytosociological survey provide an initial overview of the existing associations. Certainly, not all associations were recorded. Some small-scale communities, such as those of duckweed (*Lemna*, *Spirodela*) or small pondweeds (*Potamogeton*), were overlooked or are more common in the lake in other years.

With the current nutrient conditions in the lake and the resulting visibility depth conditions, the following associations are still expected in Lake Murten:

- *Potametum berchtoldii-pectinati* Passarge 1996
- *Lemno-Spirodeletum polyrhizae* Koch 1954
- *Lemnetum minoris* Soó ex Müller et Görs 1960
- *Parvopotamo-Zannichellietum tenuis* Koch 1926
- *Utricularietum australis* Müller et Görs 1960 nom. mut. prop.

Thanks to

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Appendix

Geographical coordinates of the fifty phytosociological surveys conducted in Lake Murten and the associated associations.

Survey No	Lat (WGS 84)	Lon (WGS 84)	Associations
1	46°57'19''	7°7'9''	*Potametum pectinati* Carstensen ex Hilbig 1971
2	46°57'3''	7°7'40''	*Phragmitetum australis* Soó 1927
3	46°56'45''	7°7'43''	*Nitellopsidetum obtusae* Dambska 1961
4	46°56'34''	7°7'51''	*Potametum pectinati* Carstensen ex Hilbig 1971
5	46°56'29''	7°7'49''	*Myriophylleto-Nupharetum* Koch ex Hueck 1931
6	46°56'29''	7°7'47''	*Charetum contrariae* Corillion 1957
7	46°55'48''	7°6'53''	*Schoenoplectetum lacustris* Eggler 1933
8	46°55'43''	7°6'45''	*Schoenoplectetum lacustris* Eggler 1933
9	46°55'35''	7°6'23''	*Schoenoplectetum lacustris* Eggler 1933
10	46°55'19''	7°5'53''	*Charetum contrariae* Corillion 1957
11	46°55'30''	7°6'16''	*Potametum lucentis* Hueck 1931
12	46°55'49''	7°6'57''	*Nitellopsidetum obtusae* Dambska 1961
13	46°54'52''	7°5'7''	*Myriophylleto-Nupharetum* Koch ex Hueck 1931
14	46°54'56''	7°5'11''	*Potametum lucentis* Hueck 1931
15	46°55'12''	7°5'17''	*Potametum pectinati* Carstensen ex Hilbig 1971
16	46°55'17''	7°5'15''	*Potametum lucentis* Hueck 1931
17	46°54'37''	7°4'36''	*Myriophylleto-Nupharetum* Koch ex Hueck 1931
18	46°54'26''	7°3'58''	*Myriophylleto-Nupharetum* Koch ex Hueck 1931
19	46°54'19''	7°3'35''	*Myriophylleto-Nupharetum* Koch ex Hueck 1931
20	46°54'23''	7°3'29''	*Potametum lucentis* Hueck 1931
21	46°54'28''	7°4'06''	*Najadetum marinae* Libbert 1932 ex Fukarek 1961
22	46°54'20''	7°3'55''	*Phragmitetum australis* Soó 1927
23	46°54'24''	7°3'29''	*Potametum perfoliati* Miljan 1933
24	46°54'22''	7°2'46''	*Myriophylleto-Nupharetum* Koch ex Hueck 1931
25	46°54'23''	7°3'25''	*Potametum pectinati* Carstensen ex Hilbig 1971
26	46°54'31''	7°2'31''	*Potametum pectinati* Carstensen ex Hilbig 1971
27	46°55'26''	7°2'12''	*Potametum pectinati* Carstensen ex Hilbig 1971
28	46°55'27''	7°2'16''	*Najadetum marinae* Libbert 1932 ex Fukarek 1961
29	46°55'27''	7°2'14''	*Myriophylleto-Nupharetum* Koch ex Hueck 1931
30	46°55'28''	7°2'20''	*Myriophylleto-Nupharetum* Koch ex Hueck 1931
31	46°55'49''	7°2'54''	*Potametum pectinati* Carstensen ex Hilbig 1971
32	46°55'57''	7°3'8''	*Potametum pectinati* Carstensen ex Hilbig 1971

Survey No	Lat (WGS 84)	Lon (WGS 84)	Associations
33	46°55’59’’	7°3’12’’	*Ceratophylletum demersi* Corillion 1957
34	46°56’02’’	7°3’18’’	*Ceratophylletum demersi* Corillion 1957
35	46°56’09’’	7°3’35’’	*Potametum lucentis* Hueck 1931
36	46°56’19’’	7°3’43’’	*Schoenoplectetum lacustris* Eggler 1933
37	46°56’23’’	7°3’49’’	*Najadetum marinae* Libbert 1932 ex Fukarek 1961
38	46°56’28’’	7°4’01’’	*Schoenoplectetum lacustris* Eggler 1933
39	46°56’31’’	7°4’07’’	*Potametum pectinati* Carstensen ex Hilbig 1971
40	46°56’33’’	7°4’09’’	*Potametum pectinati* Carstensen ex Hilbig 1971
41	46°56’45’’	7°4’53’’	*Myriophylleto-Nupharetum* Koch ex Hueck 1931
42	46°56’45’’	7°4’51’’	*Potametum lucentis* Hueck 1931
43	46°56’54’’	7°5’18’’	*Potametum lucentis* Hueck 1931
44	46°57’05’’	7°5’48’’	*Schoenoplectetum lacustris* Eggler 1933
45	46°57’02’’	7°5’42’’	*Najadetum marinae* Libbert 1932 ex Fukarek 1961
46	46°57’19’’	7°6’32’’	*Potametum perfoliati* Miljan 1933
47	46°57’24’’	7°6’57’’	*Potametum pectinati* Carstensen ex Hilbig 1971
48	46°57’12’’	7°6’55’’	*Potametum perfoliati* Miljan 1933
49	46°57’25’’	7°07’04’’	*Phragmitetum australis* Soó 1927
50	46°57’27’’	7°06’51’’	*Charetum contrariae* Corillion 1957