A22
Littorella uniflora-Lobelia dortmanna community

Synonymy
Littorella-Lobelia associes Pearsall 1918; *Eleocharitetum acicularis* Koch 1926 *p.p.*; *Isoeto-Lobelietum* (Koch 1926) Tx. 1937 *p.p.*; *Eleocharitetum multicaulis* Tüxen 1937 *p.p.*; *Juncus fluitans-Lobelia dortmanna* and *Lobelia dortmanna* associations Spence 1964; *Littorella uniflora-Lobelia dortmanna* Association Birks 1973; *Eriocaulo-Lobelietum* Br.-Bl. & Tx. 1952 *sensu* Birse 1984.

Constant species
Littorella uniflora, *Lobelia dortmanna*.

Rare species
Elatine hexandra, *Eleocharis acicularis*, *Eriocaulon septangulare*, *Isoetes setacea*, *Subularia aquatica*.

Physiognomy
The *Littorella uniflora-Lobelia dortmanna* community comprises open or closed swards of submerged or temporarily emergent vegetation, usually less than 10 cm tall, dominated by gregarious rosette plants with linear or subulate leaves. The commonest of these is *Littorella uniflora*, particularly obvious in younger stands and in shallower, wave-churned waters, sometimes sparsely scattered over stony ground, but often dominant in fine densely-packed lawns. *Lobelia dortmanna* is the only other constant and it, too, can grow in quite luxuriant profusion here, frequently exceeding *Littorella* in more sheltered, somewhat deeper waters, and revealing its presence in mid-summer with its emergent racemes of attractive lilac flowers. It is, though, not so widely distributed geographically as *Littorella* and is altogether absent from those fragmentary stands of the community found in southern England.

Also quite common throughout the range of this vegetation is *Juncus bulbosus*, often occurring in its free-floating form and sometimes forming thick tangles of slender shoots, but no other associate is frequent overall. Thus, there are occasionally some emergent shoots of *Carex rostrata*, *Equisetum fluviatile* and, in shallower waters, *Eleocharis palustris* and the more local *E. multicaulis*, but increased frequency and cover of these plants usually marks a shift to swamp vegetation. Likewise, there can be some *Myriophyllum alterniflorum* but this is strongly associated with stands in deeper and less turbulent waters, where the occasional presence of *Isoetes lacustris* or, more locally, *I. setacea* marks a transition to the zone in which these quillworts become dominant.

Other plants which occur sparsely through the community are *Scirpus fluitans*, which is often difficult to see when floating among masses of *J. bulbosus*, and *Baldellia ranunculoides*, the emergent leaves of which often get abraded by wave action. This kind of vegetation also provides a locus for the rare annual *Elatine hexandra*, for *Eleocharis acicularis* in Scotland and, in northern and western Britain, for *Subularia aquatica*. This is another very local therophyte, occasionally overwintering, that is readily overlooked among young *Littorella* but able to attain some abundance on open but stable substrates (Woodhead 1951*b*). A further rarity, *Eriocaulon septangulare*, can also be found in this community in some of its very few Scottish localities. It is a widespread plant in this sort of vegetation in western Ireland (Braun-Blanquet & Tüxen 1952), but occurs with us only in Inverness and on Coll and Skye (Perring & Farrell 1977), and even then not always among *Littorella-Lobelia* swards. On Skye, for example, where dense mats occur most commonly, it is more usually seen among stands of the *Caricetum rostratae* (Birks 1973).

Sub-communities

***Littorella uniflora* sub-community:** *Eleocharitetum multicaulis* Tüxen 1937 *p.p.*; open *Littorella-Lobelia* sociation Spence 1964; *Littorella uniflora-Lobelia dortmanna* Association Birks 1973; *Isoeto-Lobelietum* (Koch 1926) Tx. 1937, inops and *eleocharetosum* Schoof-van Pelt 1973; *Isoeto-Lobelietum* (Koch 1926)

Tx. 1937 *sensu* Birse 1984; *Eriocaulo-Lobelietum* Br.-Bl. & Tx. 1952 *sensu* Birse 1984. *Littorella* is the commonest species here, sometimes virtually the only plant in very open stands, though usually quite abundant, and generally exceeding *L. dortmanna*, which can be absent altogether. Locally, *Isoetes lacustris* is prominent but quillworts are more characteristic of the other sub-community, together with *Myriophyllum alterniflorum* which is very scarce here.

There is frequently some *Juncus bulbosus* and, among emergent plants, occasional *Carex rostrata* and *Equisetum fluviatile* are quite often accompanied here by *Eleocharis palustris* and, more locally, by *E. multicaulis*, these last two sometimes attaining high cover. In shallower waters, *Ranunculus flammula* may be prominent, together with plants like *Juncus articulatus* and *Carex nigra*. It is in this kind of *Littorella-Lobelia* vegetation that *E. septangulare* has been recorded, sometimes as a local dominant.

***Myriophyllum alterniflorum* sub-community:** *Eleocharitetum acicularis* Koch 1926 *p.p.*; *Lobelia-Littorella* and *Littorella-Juncus* sociations Spence 1964; *Isoeto-Lobelietum* (Koch 1926) Tx. 1937 *sensu* Schoof van Pelt 1973 *p.p.*, *sensu* Birse 1980. Although stands can be found here in which either *Littorella* or *L. dortmanna* is absent, the two plants are equally common overall, both can be plentiful and each may dominate. *J. bulbosus* is frequent and there is characteristically some *M. alterniflorum*, occasionally in abundance. *I. lacustris* and the much more local *I. setacea* are also weakly preferential to this sub-community and each can have high cover, particularly in transitions to quillwort swards.

Occasionally there is some emergent *C. rostrata* and *E. fluviatile* but *Eleocharis palustris* and *E. multicaulis* are only infrequently found. However, *E. acicularis* has been recorded in this vegetation in some of its Scottish localities and *Subularia aquatica* is sometimes seen here.

Habitat

The *Littorella-Lobelia* community is characteristic of the barren, stony shallows of clear and infertile standing waters. It is strongly concentrated in the north and west of Britain, where it is a widespread and common feature of lakes and pools, often extending around more exposed shores where there is some wave disturbance, but tolerating only brief exposure where water-levels fall in summer.

Through Europe as a whole, both *Littorella* and *L. dortmanna* have northerly ranges (Matthews 1955) and, in this country, they are largely confined to the north and west. This is especially true of *L. dortmanna*, which requires a cool but equable, northern oceanic climate, such that in the more frigid waters of higher altitudes and towards the warmer south of the country, stands of the community have a more fragmentary composition in which mixtures of *Littorella* and *J. bulbosus* tend to be the most obvious element. To some extent, though, the concentration of this kind of vegetation in the north and west is a reflection of the distribution of suitable substrates and waters, because clear, oligotrophic lakes are much more common in the glaciated catchments of acidic, resistant rocks that prevail there. Throughout its range, then, this is a community of infertile waters, with conductivities generally less than 200 μmho, pH usually from 5.5 to 7 and alkalinities below 25 mg l^{-1} calcium carbonate (Woodhead 1951*a*, Spence 1964, Palmer 1992, Palmer *et al.* 1992). Locally, such conditions are met in the south and east of Britain in lowland pools over base-poor, sandy substrates, as in Hatchet Pond in the New Forest and Little Sea Mere in Dorset (Ratcliffe 1977). But it is in open waters through the uplands, particularly from Snowdonia northwards, that this kind of vegetation becomes really frequent, sometimes occupying most of the bed of shallow, stony pools, but generally forming a fringe around the edge of larger lakes. Sands and gravels are the preferred substrates, sometimes with a few centimetres of organic detritus or peaty mud, but typically without any fine mineral material. Exposure to wave action in the shallows hinders the deposition of such silt as may be washed into the lakes, helping to maintain infertility.

Of the two constants, *Littorella* seems to be the earlier coloniser of bare, coarse and sometimes rather shifting substrates (Pearsall 1921) and to be the more tolerant of the periodic exposure of lake margins that occurs in drier summers. Indeed, it only flowers when its scapes, which are shorter than the foliage, are emergent. Generally, however, after initial establishment, it spreads by vegetative means, producing abundant far-creeping stolons that readily root and put up rosettes of leaves at the nodes. In this way, *Littorella* can quickly form a dense lawn and retain much of its vigour from season to season.

L. dortmanna, it seems, enters subsequently, each plant establishing from seed and needing some consolidation of a finer mineral bed, perhaps with some organic detritus caught on the surface, before it can establish firmly (Pearsall 1921, Woodhead 1951*a*). It can colonise quite shallow waters, just 10 cm or so deep, but it is generally intolerant of desiccation, being reduced in vigour when water levels are low in winter and spring, and readily killed if exposed in summer (Sylven 1903). Being never very strongly rooted, it is also rather more susceptible than is *Littorella* to the wave-turbulence of exposed shallows and, lacking any means of vegetative expansion, damage to the sward is made good only slowly. It certainly grows most luxuriantly in more sheltered and somewhat deeper waters and, unlike *Lit-*

torella, can put up its first flowers above the surface from considerable depths.

The shift in relative importance of the two constants in these contrasting situations is reflected among the associates and contributes to the definition of the two sub-communities. The *Littorella* type includes stands of the community outside the geographical range of *L. dortmanna*, but generally it is characteristic of shallower and more exposed waters, where the preferentials are those emergents able to form a sparse cover in the stony and wave-torn conditions. The *M. alterniflorum* sub-community can extend into shallows, but only where these are more sheltered, and it is usually found at somewhat greater depths, perhaps just a few decimetres below the *Littorella* type, sometimes down to 1 m or more, but where turbulence is reduced enough to allow some consolidation of the mineral base and the accumulation of a primitive organic layer. At such depths, it is able to extend on to the more exposed sides of lakes, where the shallows are too wave-churned to support even the *Littorella* sub-community. It is the stiller conditions here that favour the growth of *M. alterniflorum*, with the appearance of the quillworts reflecting the more frequent occurrence of stable substrates at some depth.

Zonation and succession

The *Littorella-Lobelia* community is a common element in the very characteristic zonations that are found in less fertile stretches of standing waters, the proportions and dispositions of the various vegetation types reflecting differences in water depth, turbulence and the character of the substrates. In more exposed and oligotrophic situations, the community is a more or less permanent feature in successions that are held in check by the harsh environmental conditions but, where accumulation of silt or organic detritus is able to proceed, this kind of vegetation is replaced by other aquatic communities or swamp.

Quite often, both sub-communities of the *Littorella-Lobelia* vegetation occur together, the *Littorella* type occupying more shallow or turbulent waters, the *M. alterniflorum* sub-community replacing it with increasing depth or shelter, moving away from the shore or shifting round to less exposed aspects. Where more or less stony substrates run on into even deeper water in upland lakes, where neither *Littorella* nor *L. dortmanna* can maintain a vigorous presence, the community often gives way to *Isoetes* vegetation, the quillworts assuming dominance and extending as sometimes pure swards to several metres depth beneath the lower limit of the *Littorella-Lobelia* community (Gay 1863, Pearsall 1921, Spence 1964).

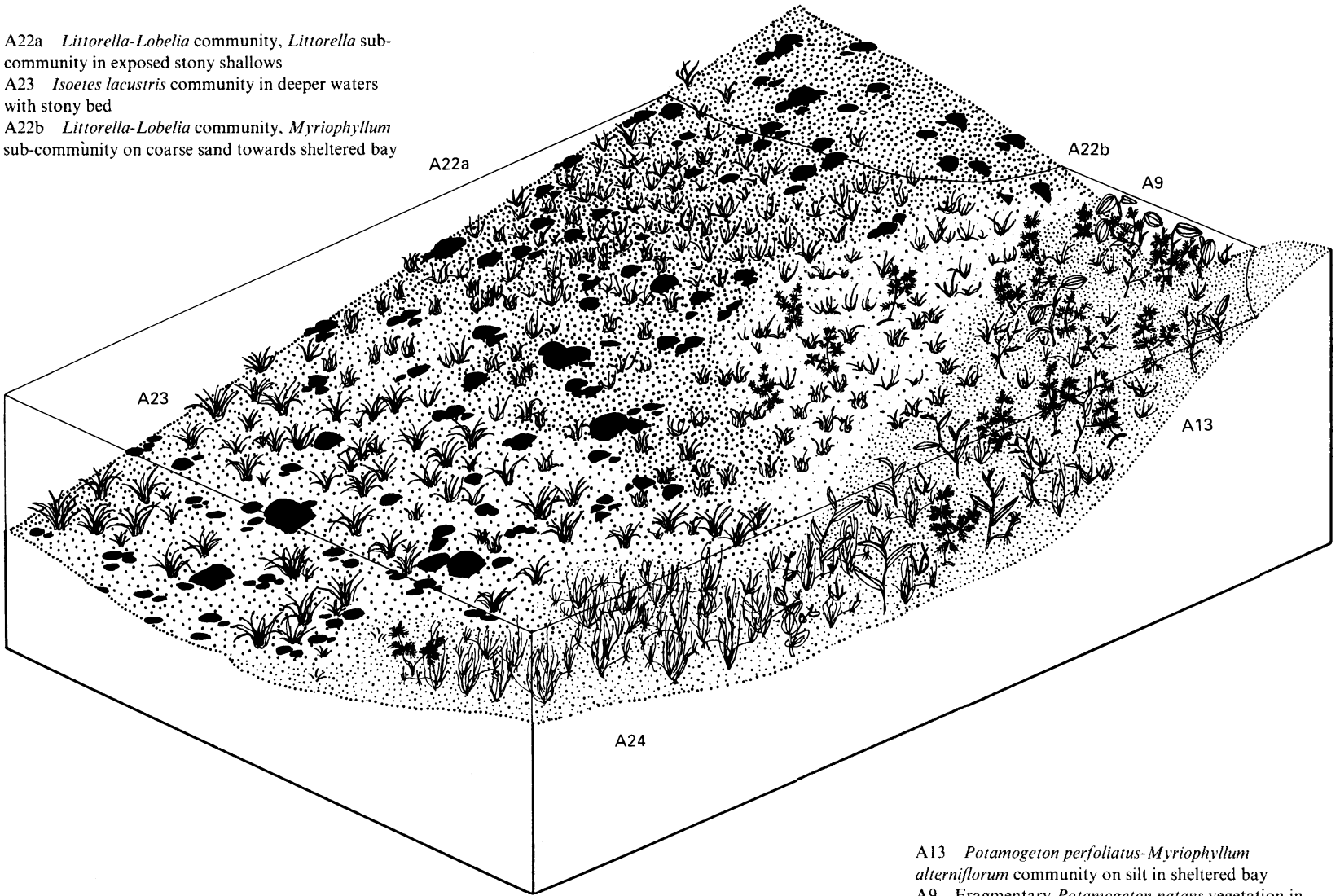
In lakes which are not quite so infertile, however, or where there are local areas of shelter and deposition of finer mineral material within the waters, the *Littorella-Lobelia* swards can give way to other communities of submerged aquatics able to take advantage of the enriched conditions (Figure 8). Where there are banks of silt along lee shores, for example, or in somewhat deeper waters beyond the wave-disturbed zone or where currents from incoming steams drop suspended, this kind of vegetation is often replaced by the *Potamogeton-M. alterniflorum* community. There, both *Littorella* and *M. alterniflorum* remain very frequent, but dominance commonly passes to pondweeds such as *Potamogeton perfoliatus*, *P. gramineus*, *P. berchtoldii*, *P. obtusifolius* or *P. pusillus*. Dense stands of *M. alterniflorum* can punctuate such patterns, often where there is a slight local increase in turbulence over sandier substrates, and there can be floating-leaved *Nymphaeetum albae* and *Potamogeton natans* vegetation with the shift to more sheltered and deeper waters. The zonations described from Cumbrian lakes by Pearsall (1918, 1921) show such variations clearly.

In more base-rich, calcareous waters, the *Littorella-Lobelia* community often maintains a presence in the more wave-torn shallows, giving way in analagous zonations to those described above to the *Potamogeton-M. spicatum* community, sometimes with *P. pectinatus* stands and floating-leaved *Nuphar lutea* vegetation. Increased eutrophication of lakes with these kinds of patterns has seen an increase in recent years in the amounts of *Elodea canadensis* and *E. nuttallii* among such assemblages.

Towards the opposite extreme, where waters become more peaty and dystrophic, as where lakes occur among or receive drainage waters from stretches of blanket mire, a common feature in Shetland and along parts of the north-west Scottish seaboard, the *Littorella-Lobelia* community can give way in sheltered shallows to the *Juncus bulbosus* vegetation. Sometimes this can be found suspended over sparse *Littorella-Lobelia* swards in peat-bound embayments with stony beds, but it is *J. bulbosus* and *M. alterniflorum* which provide the strongest continuity between the vegetation types, with species such as *Potamogeton polygonifolius*, *Utricularia vulgaris* and *Sphagnum auriculatum* becoming more abundant where there is a real shift in the character of the habitat (Spence 1964). In the striking machair lochs on South Uist and at a few localities on the nearby Scottish mainland, the *Littorella-Lobelia* community can be found in the same water bodies as both dystrophic vegetation of this kind and basiphilous pondweed assemblages on calcareous shell-sand (Ratcliffe 1977).

Where exposure restricts the accumulation of silt or organic detritus, the extent of *Littorella-Lobelia* stands can remain unchanged for decades (Spence 1964), but more sheltered and shallow waters are always prone to invasion by emergents. *Eleocharis palustris* and, more locally, *E. multicaulis* seem especially common as col-

A22a *Littorella-Lobelia* community, *Littorella* sub-community in exposed stony shallows
A23 *Isoetes lacustris* community in deeper waters with stony bed
A22b *Littorella-Lobelia* community, *Myriophyllum* sub-community on coarse sand towards sheltered bay



A13 *Potamogeton perfoliatus-Myriophyllum alterniflorum* community on silt in sheltered bay
A9 Fragmentary *Potamogeton natans* vegetation in sheltered bay
A24 *Juncus bulbosus* community on sand bar off sheltered bay

Figure 8. Generalised zonation of aquatic vegetation around the margins of an upland lake.

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onisers of more gravelly shores that are not too wave-disturbed and, around Scottish lakes, zonations to stands of the *Littorella* sub-community of the *Eleocharitetum palustris* are frequent. *Carex rostrata* and *Equisetum fluviatile* occur widely, too, extending into deeper water and being especially likely to gain a hold where there is accumulation of peaty material. Then, the *Littorella-Lobelia* community can give way to stretches of the *Caricetum rostratae* or *Equisetum* swamps from denser stands of which the smaller herbs are quickly crowded out. Where more silty material builds up, the *Phragmitetum* may replace the *Littorella-Lobelia* swards (Pearsall 1918, 1921, Spence 1964).

Distribution

The community is most widespread and common through north-west Britain from Snowdonia northwards, with much more local and fragmentary stands occurring in suitable habitats in the south of the country.

Affinities

The distinctive character of this kind of vegetation has long been recognised in Britain (Pearsall 1918, 1921), with assemblages sometimes being separated off from *Isoetes*-dominated stands (Spence 1964), sometimes not (Birks 1973, Schoof-van Pelt 1973). Even where samples have lacked any *I. lacustris* or *I. setacea* (as in Birse 1980, 1984), they have sometimes been referred to the phytosociological association erected to accommodate such swards, the *Isoeto-Lobelietum* (Koch 1926) Tx. 1937, or some amendment of it (e.g. Dierssen 1975). In this scheme, we have maintained a distinct *Isoetes* community: even though the separation between the vegetation types is not an absolute one, transitional stands being necessarily partitioned on dominance, it does reflect an important ecological contrast among assemblages of this general type.

On the other hand, our *Littorella-Lobelia* community subsumes swards with a variety of other locally abundant plants that have sometimes been used to define distinct phytosociological associations, either in Britain or in similar habitats in Ireland, as well as on the Continent. Included here, then, are stands which other authors would locate in an *Eleocharitetum multicaulis* Tx. 1937 or an *Eleocharitetum acicularis* Koch 1926 (Braun-Blanquet & Tüxen 1952, Ivimey-Cook & Proctor 1966*b*, Schoof-van Pelt 1973, White & Doyle 1982, Birse 1984) or in an *Eriocaulo-Lobelietum* Br.-Bl. & Tx. 1952 (Braun-Blanquet & Tüxen 1952, Birse 1984). Further sampling is needed to see whether this is the best way of dealing with this kind of vegetation, to check for the existence in Britain of related assemblages described from Ireland or mainland Europe, such as the *Baldellio-Littorelletum* Ivimey-Cook & Proctor 1966 and the *Salomo-Littorelletum* Westhoff 1943, and to see how the *Littorella-Lobelia* swards relate to other communities from oligotrophic shallows such as the *Hyperico-Potametum* and related vegetation described among the mires of Volume 2 of *British Plant Communities*.

Similar vegetation to that included here has been described from Scandinavia (Lohammar 1965), the Faroes (Ostenfeld 1908), Germany (Tüxen 1937), The Netherlands (Westhoff & den Held 1969, Schoof-van Pelt 1973) and south-west France (Schoof-van Pelt 1973), although in many lowland areas suitable pools have been destroyed in recent years. Schoof-van Pelt (1973) reviews the very extensive European literature about the character and classification of this kind of assemblage, which is variously accommodated in a Littorellion Koch 1926, a Lobelion dortmannae Tüxen & Dierssen 1972 or an Isoetion (Ellenberg 1978) within the Littorelletalia, the single order of the Littorelletea.

Floristic table A22

	a	b	22
Littorella uniflora	V (1–9)	V (1–8)	V (1–9)
Lobelia dortmanna	IV (1–8)	V (1–9)	V (1–9)
Eleocharis palustris	II (3–9)	I (2)	I (2–9)
Eleocharis multicaulis	II (1–6)	I (1)	I (1–6)
Ranunculus flammula	II (1–5)	I (2)	I (1–5)
Juncus articulatus	I (1–5)		I (1–5)
Carex nigra	I (1–4)		I (1–4)
Eriocaulon septangulare	I (4–7)		I (4–7)
Elatine hexandra	I (2)		I (2)
Myriophyllum alterniflorum	I (1–3)	V (1–7)	III (1–7)
Isoetes lacustris	I (2–7)	II (1–3)	II (1–7)
Isoetes setacea		I (1–2)	I (1–2)
Subularia aquatica		I (2)	I (2)
Utricularia vulgaris		I (1–3)	I (1–3)
Juncus bulbosus	III (1–6)	III (1–3)	III (1–6)
Carex rostrata	I (1–2)	I (1–2)	I (1–2)
Scirpus fluitans	I (3–5)	I (1–2)	I (1–5)
Equisetum fluviatile	I (1–2)	I (1)	I (1–2)
Baldellia ranunculoides	I (2–5)	I (5)	I (2–5)
Number of samples	31	35	66
Number of species/sample	4 (3–9)	4 (2–7)	4 (2–9)

a *Littorella uniflora* sub-community
b *Myriophyllum alterniflorum* sub-community
22 *Littorella uniflora-Lobelia dortmanna* community (total)

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