

A13

Potamogeton perfoliatus-*Myriophyllum alterniflorum* community

Synonymy

Submerged vegetation West 1910; Shallow water association Matthews 1914 *p.p.*; Linear-leaved associations Pearsall 1918 *p.p.*; *Chara*-*Myriophyllum alterniflorum* sociation Spence 1964 *p.p.*; *Potamogeton gramineus* society Spence 1964.

Constant species

Littorella uniflora, *Myriophyllum alterniflorum*, *Potamogeton gramineus*, *P. perfoliatus*.

Rare species

Callitriche hermaphroditica, *Elatine hexandra*, *E. hydro-piper*, *Isoetes setacea*, *Najas flexilis*, *Potamogeton filiformis*, *P. rutilus*, *Subularia aquatica*, *Utricularia intermedia*.

Physiognomy

The *Potamogeton perfoliatus*-*Myriophyllum alterniflorum* community subsumes the bulk of the richer and more varied pondweed assemblages in which the broader-leaved *Potamogeton perfoliatus* and *P. gramineus*, together with *Myriophyllum alterniflorum*, provide the most consistent floristic element, with never more than very occasional occurrences of either *P. pectinatus* or *M. spicatum*. Each of these constants can be abundant and luxuriant, although in more turbulent waters even their total cover is often insubstantial, and one or other species may be locally eclipsed by the dominance of some less frequent associate, or be altogether absent.

Only a few other plants are found frequently throughout the community, but there is almost always some *Littorella uniflora*, thickening up in places to form a fairly dense sward of submerged shoots among the pondweeds, and *Chara* spp. occur commonly, quite often in great abundance, with *Nitella* spp. becoming frequent too in one of the sub-communities. Then, there is generally an open floating-leaved element, with *Potamogeton natans* the most usual contributor, *P. polygonifolius* figuring in peatier places. *Polygonum*

amphibium is occasional, too, where this kind of vegetation extends into shallower marginal waters, the *Nymphaea alba*, *Nuphar lutea* and the rare *N. pumila* are sometimes found further out. Floating masses of *Juncus bulbosus* are occasionally seen and the community can provide a locus for the uncommon *Callitriche hermaphroditica*. The moss *Fontinalis antipyretica* is fairly frequent and sometimes luxuriant.

A range of other submerged pondweeds occurs in the community and differences in the frequency and abundance of these provide much of the local diversity in this vegetation. *Potamogeton pusillus*, *P. berchtoldii*, *P. obtusifolius* and, in shallower waters, the rare *P. filiformis*, are the commonest of these. Less frequent, though also occurring occasionally with some prominence, are *P. praelongus*, *P. crispus*, *P. alpinus*, *P. lucens*, *P. × zizii* (*P. lucens* × *P. gramineus*), *P. × nitens*, *P. friesii* and the rare *P. rutilus*. As with the *Potamogeton*-*M. spicatum* vegetation, locally dense growth of *Elodea canadensis* sometimes overwhelms the diversity among these plants, but this is not such a common feature here.

Associates recorded occasionally in the community include *Lobelia dortmanna*, *Isoetes lacustris* and, at a few sites, the rare *I. setacea*, *Utricularia vulgaris*, *U. minor* and the rare *U. intermedia*, *Sparganium angustifolium*, *S. minimum* and *S. emersum*, *Scirpus fluitans*, *Eleocharis acicularis*, *Callitriche hamulata*, *C. stagnalis* and *C. obtusangula*, *Ranunculus aquatilis*, *R. trichophyllus*, *R. hederaceus* and *R. peltatus*, and the rare *Najas flexilis*. Around muddy margins, there can sometimes be found the rare annuals *Subularia aquatica*, *Elatine hexandra* and *E. hydropiper*.

Sub-communities

***Potamogeton berchtoldii* sub-community.** Of the four constants, *M. alterniflorum* and *Littorella* tend to be the commonest and most abundant in this sub-community, with *P. perfoliatus* and *P. gramineus* both rather patchy in their occurrence, though showing locally high cover in

some stands. More distinctive, though, is the frequent presence of the narrow-leaved *P. berchtoldii* and *P. obtusifolius*, the former in particular being quite prominent on occasion, with *P. crispus*, *P. lucens* and *P. × zizii* sometimes accompanying the fairly common community species *P. pusillus*. *E. canadensis* and *Nitella* spp. are also strongly preferential to this kind of *Potamogeton-M. alterniflorum* vegetation, the latter often rivalling the more usual *Chara* spp. in their cover. Less frequent species found more often here include *Callitriche hamulata* and *C. obtusangula*, *Sparganium minimum* and, among the floating-leaved element, the various water-lilies. *Elatine hydropiper* has also been recorded at some sites.

***Potamogeton filiformis* sub-community:** *Chara*-*Myriophyllum alterniflorum* sociation Spence 1964 p.p.. Mixtures of all four constants in varying degrees of abundance usually dominate this vegetation with frequent and sometimes luxuriant *Chara* spp. *P. berchtoldii*, however, is no more than occasional here and rarely abundant, with *P. obtusifolius*, *E. canadensis* and *Nitella* spp. all very scarce. By contrast, *P. filiformis* becomes very common, sometimes growing densely and at high cover, with occasional *P. pusillus* and *P. friesii*. Some stands, transitional to the *Potamogeton-M. spicatum* community, also have *P. pectinatus* in some quantity, together with *M. spicatum*, *Ranunculus baudotii* and *Hippuris vulgaris*. *Zannichellia palustris* occurs occasionally and, around muddy margins, there can be some *Glyceria fluitans* trailing in.

Habitat

The *Potamogeton-M. alterniflorum* community is typical of shallow to quite deep, mesotrophic and rather base-poor waters, still or usually only gently flowing, with fine to coarse mineral beds. It is largely confined to the north and west of Britain, where suitable sites are more common and it occurs quite widely there in pools and lakes, and the middle to lower reaches of rivers. The vegetation can probably stand only very modest eutrophication but, being more remote from intensive agricultural activity, it tends to have escaped the worst effects of such influences.

This community takes in most of our richer pondweed stands from less fertile and calcareous waters than those favoured by the *Potamogeton-M. spicatum* vegetation, and by and large it has a complementary distribution. The pH and alkalinity are fairly variable but quite often fall below 7 with less than 25 mg l⁻¹ calcium carbonate and conductivities sometimes below 100 µmho (Palmer 1992, Palmer *et al.* 1992). The nutrient status is generally at most mesotrophic. Such conditions are met only locally through the lowlands of southern and eastern Britain where the community is restricted to sites like

Little Sea Mere in Dorset, a shallow lake in a stretch of heath and mire over Bagshot Beds (Ratcliffe 1977) but, to the north and west, where acidic rocks and superfcials make up the bulk of the landscape, it is a much more widespread and common feature of standing and moving waters. Even here, however, highly impoverished situations are avoided and, though the *Potamogeton-M. alterniflorum* vegetation is quite often found in the sort of moorland lochs and pools described from Scotland in the early account of West (1910), it does not favour very peaty waters and is typically rooted in the fine to moderately coarse sediments that accumulate in stiller conditions and bring some modest nutrient and base-enrichment to lakes and streams in rocky upland landscapes. The kinds of locations described from Esthwaite in the Lake District, with its catchment of Silurian grits and shales (Pearsall 1918), and from White Moss Loch on the Old Red Sandstone of Perthshire (Matthews 1914), are very typical and subsequent surveys have reported assemblages of this kind from moraine lakes like Loch Kinord in Aberdeenshire and Loch Insh in Inverness and from Loch Eye, a lake on raised beach gravels in Ross (Spence 1964, Ratcliffe 1977). There is also a striking overlap in geographical range with the *Potamogeton-M. spicatum* community along the north-western seaboard of Scotland, where close juxtaposition of limy shell-sands and peat in and around some of the machair lochs creates conditions suitable for both vegetation types in intimate association (Palmer 1992, Palmer *et al.* 1992).

In this range of sites, the most luxuriant stands of the *Potamogeton-M. alterniflorum* community are restricted to less turbulent stretches of water, away from the wave-disturbed zone along the exposed shores of lakes, some of the broader-leaved pondweeds being especially vulnerable to tearing and battering of their foliage (Haslam 1978). Of the commoner plants in this vegetation, *M. alterniflorum* and *Littorella* are considerably more tolerant, and it is they which generally predominate with a shift into more disturbed lake waters, where the sediments often become coarser and less fertile. In moving waters, too, the community is well represented only where the flow is more sluggish, thinning out to patchy *M. alterniflorum*-dominated vegetation in more shift-moving or spatey waters.

Much of the floristic contrast between the two sub-communities can be related to differences in water depth. The *P. berchtoldii* type is the more widely distributed and it extends the further, often penetrating to 3 m or so in clearer conditions, and sometimes itself showing zonal variations among the various pondweeds represented, *P. pusillus* more abundant above, *P. gramineus* extending deeper, *P. perfoliatus*, *P. praelongus*, *P. berchtoldii* and *P. obtusifolius* further still (Spence 1964). The *P. filiformis* sub-community, on the other hand, is a

more restricted type, with its rare preferential Continental Northern pondweed virtually confined to the Scottish seaboard and favouring shallow waters, often between $\frac{1}{2}$ and 1 m deep and perhaps a little more prone to turbulence. It is also this kind of *Potamogeton-M. alterniflorum* vegetation that is more often found in the transitional machair loch habitat where occasional basiphilous aquatics add further to its distinctive character.

Zonation and succession

The *Potamogeton-M. alterniflorum* community is usually found with other kinds of aquatic vegetation in characteristic zonations of less base-rich and only moderately fertile waters, becoming attenuated with increasing turbulence and giving way to other assemblages where conditions become more calcareous or eutrophic. Colonisation by emergents around the margins of waters with the community is usually fairly slow and in some places succession to swamp may be very long delayed.

Sometimes, around the sheltered shores of lakes in north-west Britain, the *Potamogeton-M. alterniflorum* vegetation is the first community of submerged aquatics encountered in moving offshore, colonising fine to fairly coarse sediments deposited in depths of 50 cm or more and free of much turbulence. Very often, however, there is in the shallows inshore, and particularly where these have a coarse sandy or gravelly bed, a zone of *Littorella-Lobelia* vegetation. As well as *Littorella*, *M. alterniflorum* may run on into such swards in some abundance blurring the boundary but, apart from occasional *P. perfoliatus*, *P. gramineus*, *P. pusillus* and *P. filiformis*, pondweeds are scarce, whereas *Lobelia dortmanna* increases greatly in frequency and cover. In shallow or moderately deep waters, the *Potamogeton-M. alterniflorum* community may continue and occupy most of the lake floor wherever suitable sediments occur, but quite commonly it is replaced below by a zone of *Isoetes lacustris* vegetation, as in the patterns described from Scottish lakes described by Spence (1964). Much more locally, usually in smaller and shallower waters, stands of the rare *I. setacea* can occur among the *Potamogeton-M. alterniflorum* community.

Then, such sequences quite frequently have dense stretches of *Chara* or *Nitella* spp. from which flowering plants are virtually absent, and these may extend both above and below the *Potamogeton-M. alterniflorum* vegetation, as in the zonation shown by Pearsall (1918) from Fold Yeat Bay in Esthwaite. In other localities, luxuriant patches of the species-poor *M. alterniflorum* community can be found among the pondweed vegetation (Spence 1964) and it is sparse stands of this plant which generally replace the *Potamogeton-M. alterniflorum* community in the faster or more spatey stretches of mesotrophic and more base-poor rivers through the

upland fringes. In somewhat more fertile, standing or sluggish waters with the *P. berchtoldii* sub-community, vigorous stands of *Elodea* vegetation may also be seen and, if eutrophication of upland lakes increases, this might be expected to overwhelm richer pondweed assemblages of this kind.

Particularly striking patterns are seen in those open waters in north-west Scotland where the *P. filiformis* sub-community occurs in the less calcareous shallows of some of the machair lochs, notably on South Uist, grading to the more basiphilous *Potamogeton-M. spicatum* vegetation where the influence of shell-sand prevails. Species such as *P. pectinatus*, *M. spicatum*, *Ranunculus baudotii* and *Hippuris* represent a transition to the *P. filiformis* sub-community of that assemblage, and where the effect of the different substrates and waters is ill-defined, the stands of the different vegetation types may intergrade. As a rule, however, *M. alterniflorum* tends to be very sparsely represented in the *Potamogeton-M. spicatum* community, with *P. gramineus* usually only occasional.

Both kinds of *Potamogeton-M. alterniflorum* vegetation can be found with a floating-leaf canopy of the *Potamogeton natans* community, with the *Nyphaeetum albae* often represented in deeper waters or, in somewhat more eutrophic situations, the *Nuphar lutea* community. The usual swamps associated with such aquatic assemblages are the *Eleocharitetum*, the *Equisetetum*, the *Caricetum rostratae*, the *Scirpetum lacustris* and the *Pragmitetum*, with usual but slow succession to the *Potentillo-Caricetum* or *Caricetum vesicariae* fen (Figure 6).

Distribution

This is largely a vegetation type of the north and west of Britain, and mostly common found in Scotland, with the *P. berchtoldii* sub-community occurring throughout the range, the *P. filiformis* type being largely confined to the far north-western seaboard.

Affinities

The community is a similarly compendious counterpart to the *Potamogeton-M. spicatum* vegetation, subsuming most of the richer pondweed assemblages previously described from our more base-poor waters (West 1910, Matthews 1914, Pearsall 1918, Tansley 1939, Spence 1964). Further sampling may reveal finer patterns of consistent floristic variation and enable the community to be related to associations like the *Potametum filiformis* Koch 1928 and the *Potametum panormitanograminei* Koch 1926 emend. Görs 1977, which seem to be the nearest Continental equivalents in the Parvopotamion alliance (Westhoff & den Held 1969, Oberdorfer 1977).

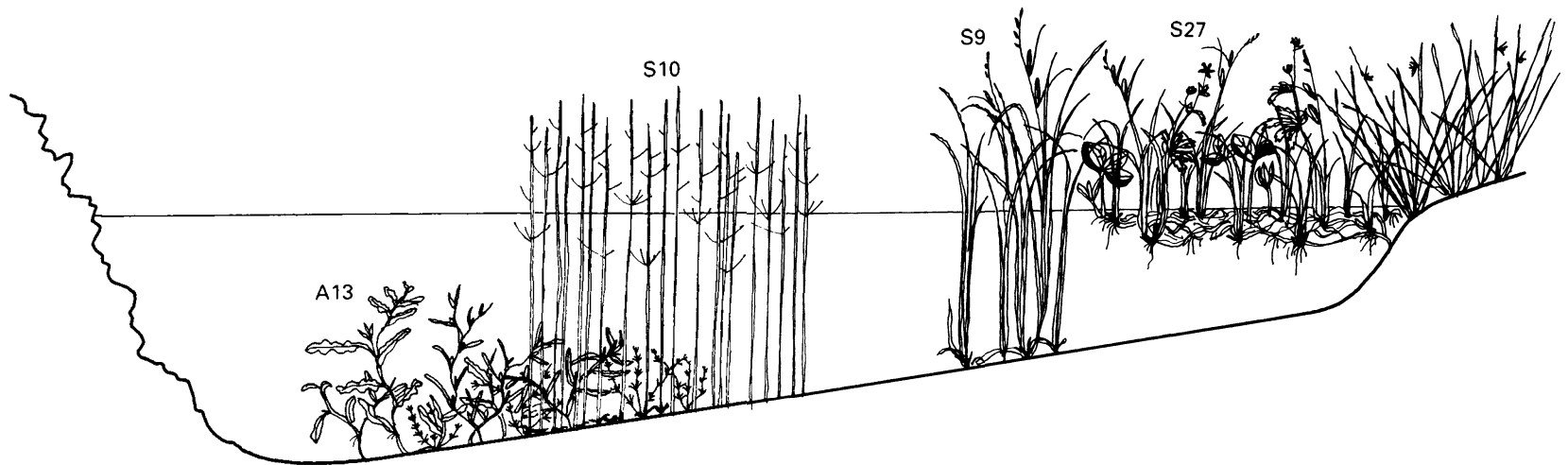


Figure 6. Zonation of aquatic, swamp and fen vegetation at Crag Lough, Northumberland.

- A13 *Potamogeton perfoliatus*-*Myriophyllum alterniflorum* community
 S10 *Equisetum fluviatile* swamp
 S9 *Caricetum rostratae* swamp
 S27 *Potentillo*-*Caricetum rostratae* fen
 with M23 *Juncus-Galium* rush-pasture on the shoreline

Floristic table A13

	a	b	13
<i>Myriophyllum alterniflorum</i>	V (1–10)	V (1–8)	V (1–10)
<i>Littorella uniflora</i>	V (1–10)	V (4–10)	V (1–10)
<i>Potamogeton perfoliatus</i>	IV (1–8)	IV (1–10)	IV (1–10)
<i>Potamogeton gramineus</i>	IV (1–10)	IV (1–10)	IV (1–10)
<i>Potamogeton berchtoldii</i>	IV (1–10)	II (1–8)	III (1–10)
<i>Nitella</i> spp.	IV (1–10)	I (1–6)	III (1–10)
<i>Elodea canadensis</i>	IV (1–10)	I (1–8)	II (1–10)
<i>Potamogeton obtusifolius</i>	III (1–10)	I (4–6)	II (1–10)
<i>Nuphar lutea</i>	II (4–6)	I (4–6)	I (4–6)
<i>Callitriche hamulata</i>	II (1–8)	I (4–6)	I (1–8)
<i>Nymphaea alba</i>	II (1–4)	I (1–4)	I (1–4)
<i>Sparganium minimum</i>	II (4–10)	I (4)	I (4–10)
<i>Potamogeton crispus</i>	II (1–10)	I (4)	I (1–10)
<i>Nuphar pumila</i>	I (1–4)		I (1–4)
<i>Elatine hydropiper</i>	I (6–8)		I (6–8)
<i>Potamogeton</i> × <i>zizii</i>	I (4–6)		I (4–6)
<i>Callitriche obtusangula</i>	I (4–8)		I (4–8)
<i>Lemna trisulca</i>	I (4–8)		I (4–8)
<i>Potamogeton lucens</i>	I (4–10)		I (4–10)
<i>Potamogeton filiformis</i>	I (1)	III (1–8)	II (1–8)
<i>Hippuris vulgaris</i>	I (1–10)	II (1–8)	I (1–8)
<i>Potamogeton pectinatus</i>	I (1–10)	II (1–8)	I (1–10)
<i>Myriophyllum spicatum</i>	I (1–6)	II (4–10)	I (1–10)
<i>Glyceria fluitans</i>	I (1–6)	II (1–6)	I (1–6)
<i>Zannichellia palustris</i>		I (1–6)	I (1–6)
<i>Potamogeton friesii</i>		I (4–6)	I (4–6)
<i>Ranunculus baudotii</i>		I (1–6)	I (1–6)
<i>Potamogeton natans</i>	III (4–10)	III (1–8)	III (1–10)
<i>Chara</i> spp.	III (1–10)	III (1–10)	III (1–10)
<i>Potamogeton pusillus</i>	II (1–8)	II (1–8)	II (1–8)
<i>Callitriche hermaphroditica</i>	II (1–10)	II (1–10)	II (1–10)
<i>Juncus bulbosus</i>	II (4–6)	II (1–8)	II (1–8)
<i>Polygonum amphibium</i>	II (1–10)	II (4–8)	II (1–10)
<i>Fontinalis antipyretica</i>	II (1–10)	II (1–8)	II (1–10)
<i>Potamogeton polygonifolius</i>	I (1–10)	I (1–4)	I (1–4)
<i>Utricularia intermedia</i>	I (4–6)	I (4)	I (4–6)
<i>Lobelia dortmanna</i>	I (1–10)	I (1–10)	I (1–10)
<i>Sparganium angustifolium</i>	I (1–10)	I (4–6)	I (1–10)
<i>Isoetes lacustris</i>	I (4–10)	I (1–6)	I (1–10)
<i>Subularia aquatica</i>	I (4–6)	I (4)	I (4–6)
<i>Najas flexilis</i>	I (8)	I (1–8)	I (1–8)
<i>Potamogeton rutilus</i>	I (4)	I (4)	I (4)
<i>Scirpus fluitans</i>	I (1–8)	I (1–6)	I (1–8)
<i>Utricularia minor</i>	I (1–6)	I (1–4)	I (1–6)
<i>Elatine hexandra</i>	I (1–10)	I (4–6)	I (1–10)

<i>Potamogeton alpinus</i>	I (1–10)	I (1–10)	I (1–10)
<i>Utricularia vulgaris</i>	I (1–8)	I (1–6)	I (1–8)
<i>Apium inundatum</i>	I (1–8)	I (1–6)	I (1–8)
<i>Potamogeton praelongus</i>	I (1–6)	I (4–6)	I (1–6)
<i>Potamogeton</i> × <i>nitens</i>	I (10)	I (1–6)	I (1–10)
<i>Eleocharis acicularis</i>	I (1–8)	I (4–8)	I (1–8)
<i>Callitriche stagnalis</i>	I (1–4)	I (1–4)	I (1–4)
<i>Lemna minor</i>	I (1–6)	I (1–6)	I (1–6)
<i>Ranunculus hederaceus</i>	I (1–4)	I (1–4)	I (1–4)
<i>Elodea nuttallii</i>	I (4–10)	I (4–8)	I (4–10)
<i>Sparganium emersum</i>	I (1–10)	I (1–4)	I (1–10)
<i>Ranunculus aquatilis</i>	I (1–8)	I (1–6)	I (1–8)
<i>Ranunculus trichophyllus</i>	I (1–6)	I (4)	I (1–6)
<i>Isoetes setacea</i>	I (1)	I (5)	I (1–5)
<i>Ranunculus peltatus</i>	I (1–10)	I (4)	I (1–10)
Number of samples	53	61	114
Number of species/sample	13 (6–26)	11 (2–21)	12 (2–26)

a *Potamogeton berchtoldii* sub-community

b *Potamogeton filiformis* sub-community

13 *Potamogeton perfoliatus*-*Myriophyllum alterniflorum* community (total)