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Potamogeton pectinatus-Myriophyllum spicatum community

Synonymy

Slow-moving water community Tansley 1911; Submerged-leaf association Pallis 1911; Moderate current vegetation Butcher 1933; Submerged community Tansley 1939; *Potamogeton filiformis-Chara* sociation Spence 1964; *Potametum pectinato-perfoliati* Den Hartog & Segal 1964; *Potamogeton perfoliatus* Gesellschaft Oberdorfer 1977.

Constant species

Myriophyllum spicatum, Potamogeton pectinatus.

Rare species

Potamogeton filiformis, P. trichoides, Ranunculus baudotii.

Physiognomy

The Potamogeton pectinatus-Myriophyllum spicatum community includes most of the richer and more diverse pondweed vegetation in which Potamogeton pectinatus and Myriophyllum spicatum play a prominent role. Usually, both these plants are present, often in some abundance by mid-summer, but stands in which just one or the other occurs, together with the characteristic community associates, can also be placed here. P. pectinatus is particularly striking where the vegetation extends into more nutrient-rich, standing or slow-moving waters, where it can make rapid growth in early summer from its overwintering tuberous buds or fruits, forming bushy clumps up to 2 m or so long. M. spicatum can also grow luxuriantly in this community, and tends to perform rather better than P. pectinatus where the flow is somewhat faster or has occasional spates, so it is often the more abundant plant where the vegetation extends into the moderately swift reaches of rivers. M. alterniflorum, however, is very scarce here and only occurs where there is some influence from more basepoor and oligotrophic waters, where the community begins to grade to the Potamogeton-M. alterniflorum vegetation characteristic of such situations. The rare M.

verticillatum occurs very locally in stiller waters, mostly in eastern England.

Other Potamogeton spp. occur with varying frequency and abundance in the community and further sampling might allow the definition of additional vegetation types of this general kind in which various of these pondweeds occur with more consistent prominence. Comparison with earlier accounts, however, suggests that local dominance among these associates was once much more widespread than is now the case (Pallis 1911, Tansley 1911, Pearsall 1921, Butcher 1933). P. pusillus, a linear-leaved pondweed like P. pectinatus, though not such a common plant, remains fairly frequent throughout, particularly in standing and more slow-moving waters, but P. crispus and P. lucens, both broad-leaved species, seem to be only occasional these days. More striking still is the relative scarcity of P. perfoliatus, another broad-leaved pondweed, which appears to be nothing like so common as previously, though, as with these other species, it can still be very abundant in some stands, occasionally to the exclusion of *P. pectinatus*.

P. natans sometimes provides a floating-leaved element to the vegetation, and there is occasionally some P. berchtoldii and, less often, P. obtusifolius, P. praelongus, P. × nitens, P. alpinus or the rare P. trichoides or P. compressus. Another rarity, P. filiformis, is particularly characteristic of one sub-community in shallower waters in Scotland, and in this kind of vegetation, too, P. friesii and P. gramineus have occasionally been recorded.

Locally luxuriant growth of these species can also be accommodated within the broad compass of the community, but just as commonly now it is the abundance of *Elodea* spp. among the *P. pectinatus* and *M. spicatum* that is the most striking feature of the vegetation. The commonest of these American introductions, *E. canadensis*, first recorded with certainty in Britain in the 1840s, is the most widespread here, varying from just occasional to very frequent in the different sub-communities and often growing very den-

sely, but E. nuttallii can also occur in considerable quantity. Not distinguished in this country until 1966, this plant has now been found quite widely in England, occasionally in Wales and Scotland, and appears to be spreading, perhaps being able to oust E. canadensis under certain conditions (Simpson 1984, 1986). It has certainly been recorded preferentially here in one particular kind of Potamogeton-M. spicatum vegetation, where its more widespread relative is less frequent, but further sampling is needed to clarify where the ecological affinities of the plants are different, and much care needs to be taken to distinguish them because both show great phenotypic plasticity (Simpson 1988). Vegetation with the much rarer third species, E. callitrichoides, now thought extant in only two localities (Simpson 1986), has not been sampled.

Other plants frequent throughout this vegetation are few, but there is quite often some Polygonum amphibium and Sparganium emersum, and many stands have an abundance of *Chara* spp., though these have not been distinguished from one another in the sampling. Nitella spp. are much scarcer, though can show local prominence in some places. Occasionals include Callitriche stagnalis, C. hermaphroditica, C. hamulata, C. obtusangula, Ranunculus peltatus, R. trichophyllus, Zannichellia palustris, Ceratophyllum demersum, Utricularia vulgaris, Juncus bulbosus, Apium inundatum and the moss Fontinalis antipyretica. Nuphar lutea, Nymphaea alba and, more locally, Nymphoides peltata can occur as an open cover of floating-leaved vegetation, sometimes with Lemna minor and Hydrocharis morsus-ranae, and shoots of Glyceria fluitans or G. plicata can trail into shallows from water margins.

Sub-communities

Potamogeton pusillus sub-community. Mixtures of *P. pectinatus* and *M. spicatum*, together with the preferential *P. pusillus* and *E. nuttallii*, form the bulk of the cover here, with *Chara* spp. also rather more frequent than elsewhere in the community, and *P. lucens* occurring occasionally. *E. canadensis*, *Sparganium emersum* and *Polygonum amphibium* are all fairly common and there is sometimes a little *P. crispus*, *P. trichoides* and *Ranunculus circinatus*.

Elodea canadensis sub-community. P. pusillus remains fairly frequent in this sub-community, but along with P. pectinatus the commonest pondweeds are usually P. crispus and P. natans with more occasional P. berchtoldii, P. perfoliatus and P. obtusifolius. M. spicatum is still constant; like each of the Potamogeton spp., it can grow luxuriantly here. Very often, though, E. canadensis is the most abundant plant, only rarely with, or replaced by, E. nuttallii. There is sometimes a lot of Lemna trisulca

entangled among the pondweeds and Ranunculus circinatus occurs rather more often here than elsewhere in the community. Very occasional, but confined to this kind of Potamogeton-M. spicatum vegetation, are the rarities P. compressus, occurring scattered through the Midlands and East Anglia, Stratiotes aloides in eastern England, Luronium natans towards the north-west of England and in Wales, and the annual Elatine hydropiper, found in just a very few localities across the country.

Among the community associates, *Polygonum amphibium* and *Sparganium emersum* are fairly frequent, with occasional *Zannichellia*, *Juncus bulbosus*, *Utricularia vulgaris*, *Callitriche stagnalis*, *C. hamulata*, *Ceratophyllum demersum* and *Glyceria fluitans*.

Potamogeton filiformis sub-community: Potamogeton filiformis-Chara sociation Spence 1964. Both P. pectinatus and M. spicatum are constant here and many stands have an abundance of Chara spp. Particularly distinctive, however, is the frequency and local prominence of the rare P. filiformis, especially abundant in shallow waters, with occasional P. friesii, P. gramineus and P. polygonifolius extending deeper. P. pusillus remains quite common in waters of moderate depth and, among other pondweeds of the community, P. berchtoldii, P. perfoliatus, P. obtusifolius, P. crispus and P. natans all occur quite often and each can show local dominance, particularly in deeper waters. Elodea spp. are poorly represented but there is very often some floating-leaved Polygonum amphibium.

Other preferential features of this vegetation are the high frequency of Hippuris vulgaris and Littorella uniflora with common Ranunculus baudotii and occasional R. trichophyllus, Callitriche stagnalis, C. hermaphroditica and Zannichellia palustris. Myriophyllum alterniflorum is confined to this kind of Potamogeton-M. spicatum vegetation, and there can be sparse records for Lobelia dortmanna or Ruppia spiralis. Among the general community associates, Apium inundatum, Fontinalis antipyretica and Juncus bulbosus are fairly common.

Habitat

The *Potamogeton-M. spicatum* community is best developed on finer mineral substrates in clear, standing to moderately fast-moving waters, which are generally mesotrophic to eutrophic and base-rich, sometimes marly, occasionally slightly saline. It occurs widely throughout Britain, mostly in the lowlands, being found in dykes, canals, ponds and lakes, where it can penetrate to considerable depths, and extending into streams and rivers where these are not too swift or spatey. This kind of aquatic vegetation can stand a modest amount of eutrophication, but it has become increasingly impover-

ished and local with the greater pollution and turbidity of many sites.

The community subsumes the bulk of our more diverse Potamogeton vegetation in fertile and base-rich waters. The pH and alkalinity vary somewhat among the different sub-communities, but are generally between 7 and 8.5 with 30-125 mg l⁻¹ calcium carbonate and conductivities of 200-1000 μmho (Palmer 1992, Palmer et al. 1992). Such conditions are quite widely met through the lowlands of Britain in waters occurring on, or fed by drainage from, less acidic rocks and superficials and rich examples of this kind of vegetation were described in early studies from the Norfolk Broads and streams and rivers flowing from the East Anglian Chalk (Pallis 1911, Tansley 1911, Butcher 1933). Stands have been noted subsequently in many open waters in England, including artificial examples like the Tring Reservoirs in Hertfordshire, the Chew Valley and Blagdon reservoirs in Somerset and the flooded gravel pits of the Cotswold Water Park, and the sluggish to moderately fast-flowing reaches of rivers such as the Hampshire Avon and the Wye (Ratcliffe 1977). The community also occurs in some stretches of canal, like the Prees Branch of the Shropshire Union, and in dykes, though here stands are often fragmentary (e.g. Pevensey Levels Survey 1986). Towards the west and north, suitable sites become scarcer, though the local occurrence of lakes on more calcareous drift, as at Llangorse in the Brecon Beacons and Hornsea Mere in Yorkshire, or on limestone, as at Malham Tarn and over the Durness rocks of Sutherland, can provide congenial habitats, and the slower reaches of more eutrophic rivers such as the Tweed also have this vegetation (Ratcliffe 1977). Deposition of fine mineral material in waters that are not generally very fertile or base-rich can also create locally suitable conditions, as in the Cumbrian lakes described by Pearsall (1918, 1921). Particularly striking, too, along the north-western seaboard of Scotland are the sites provided for the community in open waters influenced by calcareous wind-blown sands. These do occur locally elsewhere in Britain, as at Kenfig Pool in Glamorgan, Llyn Coron in Anglesey and the Loch of Strathbeg in Aberdeenshire, but it is in the pools and lakes on the machair landscape of the Isles, notably South Uist, and at scattered mainland localities in Ross and Sutherland, that the stands are the most extensive and richly developed.

In these various kinds of sites, the richer and more luxuriant stands of the *Potamogeton-M. spicatum* community are confined to the quieter stretches of water with beds of finer mineral materials, away from the wave-disturbed zone on exposed shores in lakes and pools, and the swift or more spatey reaches of moving waters. In fact, the two constants of the community are somewhat more tolerant of turbulent conditions than

most of the other associates of this vegetation, and it is small individuals of these species which often characterise the open cover in more disturbed situations. *P. pectinatus* is quite susceptible to uprooting or damage to its shoots when the plants are small in the spring or where bushy growth experiences summer storm flows, but it readily regrows, and it will tolerate the moderately turbid conditions that can develop with bed disturbance. *M. spicatum* is shallow-rooted and likely to be dislodged with little force, but it can remain vigorous in faster flows than *P. pectinatus* and will survive long from battered fragments (Haslam 1978).

In less turbulent situations, various of the other *Potamogeton* spp. can make abundant growth in this community, sometimes forming the locally dense patches of one or two pondweeds that were described as consocies or sociations in earlier accounts (Pearsall 1921, Spence 1964). And, where there is some gradation in depth of the waters, these may be disposed, within the overall cover of the vegetation, in a zoned fashion. Species such as *P. filiformis* and, to a lesser extent, *P. pusillus* are confined to shallower situations, *P. pectinatus* extending further, *P. perfoliatus*, *P. gramineus*, *P. praelongus* and *P. obtusifolius* penetrating to the greatest depths reached by the community (Pearsall 1918, 1921, Tansley 1939, Spence 1964).

Very often now, though, such local patterning is overwhelmed by the general abundance throughout of P. pectinatus or quite commonly by dense growth of one or other of the *Elodea* spp., and both the *P. pusillus* and Elodea sub-communities contain many stands of this kind in which the associate species are reduced to sparse individuals. There is little doubt that such a change reflects in part the increasing eutrophication of open waters from such sources as agricultural run-off and sewage discharge. P. pectinatus, for example, is very tolerant of such enrichment and will actually grow more luxuriantly in moderately polluted and turbid waters, provided these are not too shallow or fast-moving (Haslam 1978). Richer waters which are relatively unpolluted, clear and sluggish or standing also provide a very congenial medium for the opportunistic expansion among this vegetation of E. canadensis (Haslam 1978, Simpson 1983, 1984). This appears to have spread through much of its existing range in Britain by the middle of the present century, though there is some evidence that it is still continuing its advance in less oligotrophic waters in northern Scotland (Simpson 1983). E. nuttallii remains much less widespread, though it seems to have very similar ecological requirements to E. canadensis. It is possible, however, that it fares the better in less nutrient-rich situations, and it may be able to oust E. canadensis where it invaded subsequently (Simpson 1983, 1984). Trophic differences may play some part in the floristic contrasts between the P. pusillus and Elodea sub-communities, although the former also appears to be more characteristic of shallower and perhaps more sluggish waters than the latter.

These two kinds of *Potamogeton-M. spicatum* vegetation, particularly the *Elodea* sub-community, occur widely through lowland England, with less common occurrences in Wales and southern and eastern Scotland. The P. filiformis sub-community, on the other hand, is very much confined to the seaboard of Scotland, especially towards the west, largely beyond the present range of the *Elodea* spp., and best developed of all in the pools and lochs of the machair. Here, there is not only the phytogeographic peculiarity of the occurrence of the rare Continental Northern pondweed P. filiformis, but also a more frequent diversity among the abundant associates, particularly those tolerant of more calcareous conditions. In sites like lochs Bornish, Upper Kildonan, Torornish, Stilligarry and Grogarry on South Uist, for example, the pH is often at the highest levels associated with the community, frequently over 8, with conductivities often over 500 μmho (Palmer 1992, Palmer et al. 1992). The waters are generally clear and often marly, and in exposed situations there is the added complication of some saline influence from salt-laden winds or percolating ground waters. There is often considerable variation within and between stands in the abundance of the plants, and zonations in the deepening waters over shelving shores are more frequently evident here than in the other sub-communities. P. filiformis commonly dominates in the shallows, P. pectinatus and P. gramineus becoming prominent beyond this, P. obtusifolius, P. perfoliatus and P. praelongus usually penetrating furthest, to 3 m or so where the waters are particularly clear and still. This kind of vegetation also provides a frequent locus for Hippurus vulgaris and Ranunculus baudotii in some of their few Scottish localities, the former reaching depths of 1 m or more in extreme cases.

Zonation and succession

The Potamogeton-M. spicatum community is found alone, or with other submerged aquatic vegetation, extending to the limits of colonisation in less turbulent, base-rich waters, thinning out in more exposed situations and being replaced by other communities where conditions become less calcareous and eutrophic. Open covers of floating or floating-leaved aquatics can be found on the surface above the community and in shallower waters there can be invasion by swamp vegetation.

Through the lowlands of southern and eastern Britain, the *P. pusillus* and *Elodea* sub-communities can be found in less polluted, sluggish waters grading to locally dense stands of *Elodea* vegetation in which associate species are very few and sparse, or in shaded situations

to luxuriant patches of the Ceratophylletum demersi. Very commonly, too, especially with the Elodea subcommunity, there is an associated floating mat of the Lemnetum minoris or sometimes an open cover of the Polygonum amphibium, Potamogeton natans or Nuphar lutea floating-leaved vegetation. The most frequently associated swamps of open-water transitions from such aquatic assemblages are the Sparganietum erecti, the Typhetum latifoliae, the Phragmitetum and the Glycerietum maximae, with the Caricetum ripariae and Scirpetum lacustris more occasionally represented. Around the shelving water margins of small pools, dykes and canals and along the banks of streams, various kinds of Glycerio-Sparganion vegetation can also be found trailing out into the Potamogeton-M. spicatum community.

Where there is an increase in turbulence in such waters, shifting into wave-disturbed zones or into more fast-moving or spatey streams, the *P. pusillus* and *Elodea* sub-communities become increasingly sparse in cover, and impoverished in their species content, such that just scattered, puny plants of *P. pectinatus* and *M. spicatum* finally remain. Further upstream in base-rich moving waters, these kinds of vegetation can be replaced by the *Ranunculetum fluitantis*, the *Ranunculus penicillatus* community or *Callitriche* stands.

Patterns involving the P. filiformis sub-community in its distinctive north-west Scottish sites are of a rather different character, particularly where there is some influence within the same loch or pool of peaty, basepoor waters, quite a common and very striking feature over parts of the machair. Here, such submerged vegetation as the *Elodea* communities and the *Ceratophylle*tum demersi are rarely present, although where there is some saline influence, the *Potamogeton-M. spicatum* vegetation may give way to the Ruppietum maritimae in which such species as P. pectinatus, Ranunculus baudotii, Hippuris vulgaris and Zannichellia palustris maintain some representation. More often, with the decreasing influence of shell-sand, there is a fall in pH and conductivity of the waters and the community is replaced by the Potamogeton-M. alterniflorum vegetation. The P. filiformis sub-community can be seen as transitional to this assemblage and, indeed, P. pectinatus, P. filiformis, P. pusillus and P. natans can run on into it at moderately high frequency and with some local abundance. Typically, though, it is P. perfoliatus and P. gramineus which provide the most consistent element of the less calcicolous vegetation, together with M. alterniflorum, which almost completely replaces M. spicatum. In some places, where peaty shallows pass quite suddenly to shelly beds further out, the switch from one vegetation type to the other is quite sharp, but often the influence of the different substrates is less well defined, when transitions can be extensive. There is often, too, some Littorella uniflora amongst both assemblages, which adds to the continuity of the pattern, and this can thicken up locally in zonations to the *Littorella-Lobelia* community, especially where the substrate becomes gravelly. A floating-leaved element may be represented by the *Nymphaeetum albae* or the *Potamogeton natans* community and the usual swamps associated with the margins of these waters are the *Eleocharitetum palustris*, the *Equisetetum fluviatilis*, the *Caricetum rostratae* or, occasionally, the *Phragmitetum*.

Such sites have, for the most part, been spared any marked influence of eutrophication or pollution but, elsewhere, the *P. pusillus* and *Elodea* sub-communities have often been replaced by impoverished *P. pectinatus* vegetation with increased richness and contamination of the waters.

Distribution

This kind of vegetation is widespread but local throughout lowland England with more occasional stands in Wales and Scotland. The *P. filiformis* sub-community is largely confined to the western seaboard of Scotland, with the other types occurring through the rest of the range.

Affinities

The Potamogeton-M. spicatum community subsumes most of the richer Potamogeton vegetation of our most base-rich waters. It is clearly less diverse than some of the pondweed assemblages described in early accounts (Pallis 1911, Tansley 1911, 1939, Butcher 1933), but this is in part a real reflection of the changes that have occurred among this kind of aquatic vegetation in recent years. Further sampling is needed to see whether a range of discrete communities could be characterised from among the variation that is included here, and to relate this kind of vegetation to associations described from the Continent by den Hartog & Segal (1964) and Oberdorfer (1977) and now generally placed in the Parvopotamion alliance.

Floristic table A11

	a	b	c	11
Potamogeton pectinatus	IV (1-10)	IV (1-10)	IV (1-10)	IV (1-10)
Myriophyllum spicatum	IV (1–8)	IV (1-8)	IV (1–10)	IV (1-10)
Chara spp.	IV (1-8)	II (1–10)	III (1–10)	III (1–10)
Potamogeton pusillus	IV (1-10)	II (1-10)	II (1–10)	II (1-10)
Elodea nuttallii	III (1-10)	I (1–10)		I (1–10)
Potamogeton lucens	II (1-10)	I (1–6)		I (1–10)
Elodea canadensis	II (4–8)	IV (1-10)	I (4-10)	III (1-10)
Potamogeton crispus	I (4–6)	III (1-10)	II (1–10)	II (1-10)
Potamogeton natans	I (1-5)	III (1-10)	II (1-5)	II (1–10)
Lemna trisulca		II (1–10)	I (1–8)	I (1–10)
Ranunculus circinatus	I (1–8)	II (1-10)	I (4)	I (1-10)
Elatine hydropiper		I (1–8)		I (1–8)
Luronium natans		I (8–10)		I (8-10)
Stratiotes aloides		I (4–8)		I (4–8)
Potamogeton compressus		I (1–10)		I (1-10)
Potamogeton filiformis		I (10)	IV (1-8)	II (1–10)
Hippuris vulgaris		I (4-10)	IV (1-5)	II (1-10)
Ranunculus baudotii		I (4-6)	III (1-10)	I (1-10)
Potamogeton friesii	I (4)	I (4–10)	II (1-10)	I (1–10)
Zannichellia palustris	I (4)	I (1-10)	II (1-10)	I (1–10)
Littorella uniflora	I (6)	I (46)	III (4–10)	II (4-10)
Callitriche stagnalis	I (4)	I (1–8)	II (1–8)	I (1–8)
Callitriche hermaphroditica		I (10)	II (4–8)	I (4–10)
Ranunculus trichophyllus		I (4–10)	II (1–10)	I (1–10)
Potamogeton gramineus		I (1)	II (1-10)	I (1–10)

Floristic table A11 (cont.)

	a	b	c	11
Myriophyllum alterniflorum			I (1–8)	I (1-8)
Lobelia dortmanna			I (4-6)	I (4–6)
Ruppia spiralis			I (1-5)	I (1-5)
Polygonum amphibium	II (1–4)	III (1-10)	III (1–10)	III (1–10)
Sparganium emersum	II (1 -4)	II (1-5)	I (1-4)	II (1-5)
Potamogeton berchtoldii	I (1–8)	II (1-10)	II (1-10)	II (1-10)
Potamogeton perfoliatus	I (1-10)	II (4–10)	II (1-10)	II (1-10)
Nitella spp.	I (8-10)	1 (1-10)	I (1-10)	I (1-10)
Glyceria fluitans	I (1–4)	l (1–6)	I (1-8)	I (1–8)
Fontinalis antipyretica	I (1-6)	I (1-10)	I (1-10)	I (1-10)
Potamogeton obtusifolius	I (6)	I (1-10)	I (1-10)	I (1-10)
Nuphar lutea	I (1-4)	I (1-5)	I (1-4)	I (1-5)
Lemna minor	I (1-3)	I (1–4)	I (1-4)	I (1-4)
Potamogeton trichoides	I (1-4)	I (6-10)	I (1)	I (1-10)
Nymphaea alba	I (1–4)	I (2-4)	I (2-4)	I (1-4)
Callitriche hamulata	I (4)	I (1-10)	I (1)	I (1-10)
Utricularia vulgaris	I (8)	I (4–6)	I (1–4)	I (1–6)
Ranunculus peltatus	I (4)	I (6)	I (1-2)	I (1-6)
Ceratophyllum demersum	I (1-6)	I (4-10)	I (4)	I (1-10)
Callitriche platycarpa	I (4)	I (1-4)	I (4)	I (1-4)
Glyceria plicata	I (1-4)	I (1–4)		I (1-4)
Hydrocharis morsus-ranae	I (4)	I (4–8)		I (4–8)
Juncus bulbosus	I (4)	I (1-10)	I (4-10)	I (1-10)
Nymphoides peltata	1 (8)	I (4)		I (4–8)
Potamogeton alpinus		I (1-6)	I (1-6)	I (1-6)
Apium inundatum		I (4–8)	I (1-4)	I (1–8)
Potamogeton praelongus		I (8)	I (1-8)	I (1-8)
Potamogeton × nitens	I (4)		I (4–6)	I (4–6)
Callitriche obtusangula		I (4)	I (4–6)	I (4-6)
Potamogeton polygonifolius		I (6)	I (1–4)	I (1–6)
Ranunculus omiophyllus		I (4)	I (1)	I (1-4)
Oenanthe aquatica		I (1)	I (1–4)	I (1-4)
Number of samples	74	73	100	247
Number of species/sample	7 (2–10)	10 (4–16)	8 (4–21)	8 (2-21)

a Potamogeton pusillus sub-community

b Elodea canadensis sub-community

c Potamogeton filiformis sub-community

¹¹ Potamogeton pectinatus-Myriophyllum spicatum community (total)