A23
Isoetes lacustris/setacea community

Synonymy
Isoetes lacustris consocies Pearsall 1918, 1921; *Isoetes lacustris* society Spence 1964; *Isoeto-Lobelietum* (Koch 1926) Tx. 1937 *sensu* Schoof-van Pelt 1973 *p.p.*

Constant species
Isoetes lacustris or *I. setacea.*

Rare species
Isoetes lacustris, *Subularia aquatica.*

Physiognomy
The *Isoetes* community comprises submerged swards dominated by the aquatic pteridophytes, *Isoetes lacustris* and/or the more local *I. setacea.* Both species are gregarious perennials, *I. lacustris* in particular forming extensive dense stands, but sparser covers of scattered individuals occur, and *I. setacea* is often found in quite small, sporadically distributed patches. The growth habit is rosette-like, the plants bearing numerous quill-like leaves, stiff and brittle in *I. lacustris*, rather more spreading and flexible in *I. setacea* and, when the individuals are closely packed, the overall impression is of an uneven lawn. The size of the plants varies considerably with the depth and turbulence of the waters, and there is perhaps also some measure of genetic difference between what are often very isolated populations, but *I. lacustris* is generally the larger species, the leaves reaching up to 25 cm or more, with those of *I. setacea* usually less than 15 cm. Nonetheless, where the two quillworts occur together, as is locally the case, the smaller species, commonly the minor element in the sward, is easily overlooked (Page 1982*a*, *b*).

Very many stands of this kind of vegetation are pure or almost so, but a number of associates occur occasionally and some of these can be locally abundant, especially where the *Isoetes* swards extend into shallower waters. *Littorella uniflora* and *Lobelia dortmanna*, for example, often occur in the same lakes as the community and can sometimes be found sparsely distributed among the quillworts, when they are hard to distinguish from them. Then, there is quite frequently some *Myriophyllum alterniflorum* or free-floating *Juncus bulbosus*, with occasional patches of *Potamogeton perfoliatus*, *P. berchtoldii*, *P. crispus*, *P. obtusifolius* or, not recorded here but regarded as characteristic by Page (1982*a*), *P. alpinus*. *Callitriche hamulata*, *C. hermaphroditica*, *Sparganium angustifolium*, *Scirpus fluitans*, *Utricularia vulgaris* agg. and the rare *Subularia aquatica* can also be seen, with *Elodea canadensis* or *E. nuttallii* locally prominent in some more fertile waters. *Nitella* spp. or, less commonly, *Chara* spp. are sometimes abundant too.

Habitat
Isoetes vegetation is characteristic of barren, stony substrates in the clear, deep waters of less fertile lakes through north-west Britain.

Both species have what could be described as a northern sub-Atlantic distribution in this country (Jermy *et al.* 1978), with few stations outside the very wettest of our cooler upland regions. *I. lacustris* has been found much more commonly than *I. setacea*, occurring widely through the north-west from Snowdonia northwards and continuing to somewhat higher altitudes, up to more than 800 m in places (Page 1982*b*). *I. setacea* extends a little further into suitable habitats in the warmer south of the country, as in the New Forest and around Dartmoor and Exmoor, but is much the more scarce of the two in the Lake District and southern Scotland. It has also been recorded more locally than *I. lacustris* through the Scottish Highlands, though further sampling may show that it is at least as common there (Jermy *et al.* 1978).

The concentration of this kind of vegetation in the north-west is a reflection of the frequency there of larger bodies of less fertile standing waters in very rainy, often barren landscapes made up largely of acidic, resistant rocks (Page 1982*a*, *b*). In general, these swards occur in big and deep-watered lakes of glacial basins, scoured clean in the past and with little input of finer and more

fertile mineral material from the young, often torrential feeder streams (Pearsall 1918, Page 1982*a*, *b*). The substrates are usually sands or gravels, firmly consolidated into a stable bed, sometimes with scattered, occasionally with crowded, boulders. Characteristically, there is hardly any deposition of silt, though a centimetre or two of fine, peaty detritus may be found and *I. lacustris* can occur on deep nekron muds (Page 1982*b*).

In such situations, *Isoetes* swards are typically the most deeply penetrating of all vascular aquatic communities, and the usual dominant on such stony beds below 2 m, extending much further where the waters are clear, as they often are in these lakes (West 1910, Pearsall 1918, Spence 1964). *I. lacustris* can grow quite vigorously down to about 6 m, with *I. setacea* generally occurring at less than 4 m depth, often under 2 m (Page 1982*b*). In shallower waters, wave disturbance in autumn and winter storms may be important in promoting the shedding of the quills that is essential for the rupture of the basal sporangia, while in quieter and deeper waters natural decay, perhaps aided by the foraging of fish or waterfowl, may help dispersal and reproduction (Page 1982*b*). Extending more often into shallows than *I. lacustris*, *I. setacea* is the more likely species to be exposed when water levels fall in drier summers, but frequently this kind of vegetation is never seen emergent and all the casual observer knows of the occurrence of the swards beneath the waters is the accumulation of shed quills along sheltered strandlines at the end of the season.

In these generally infertile conditions, and especially at greater depths where light attenuation is substantial, few other vascular plants can survive, such that many stands of this vegetation are very species-poor. Conversely, the limit to growth of the quillworts in shallower waters, particularly where these are sheltered, and the general scarcity of the community in more eutrophic, silted lakes, even in deeper parts, is probably a reflection of the sensitivity of the *Isoetes* spp. to competition from other vascular plants (Page 1982*b*). Furthermore, although Seddon (1965) found no difference in the quality of Welsh waters with *I. lacustris* and *I. setacea*, it now seems that the latter is more closely confined to oligotrophic lakes of low alkalinity (Page 1982*b*) and this may indicate some variation in competitive ability between the two species, the former that much more unable to survive where more mesophytic aquatics can also thrive. Certainly, although *I. setacea* sometimes occurs among *I. lacustris* in more fertile lakes, the two species are usually found growing separately.

It is possible that the populations of the two quillworts in different lakes represent long-isolated, inbreeding communities (Manton 1950), although new localities can be colonised: *I. setacea*, for example, has been found in some isolated man-made reservoirs (Stokoe 1978). How these heterosporous plants are dispersed over appreciable distances is uncertain, but carriage of the spores on bird feathers seems a possibility (Page 1982*a*, *b*).

Zonation and succession

The *Isoetes* community typically occurs at the limit of vascular plant colonisation on the stony beds of infertile lakes, petering out where light attenuation becomes limiting and giving way to other kinds of aquatic vegetation with changes in depth of the waters and the character of the substrates. In the generally barren conditions favoured by the quillworts, these swards can be a more or less permanent feature, but any tendency to silting or accumulation of organic detritus leads to their replacement by other communities.

Very often, where there is a continuous stretch of sandy or gravelly substrates from the shallows to deeper parts of oligotrophic waters, stands of *Isoetes* replace the *Littorella-Lobelia* vegetation in moving away from the shore. Transitions between the communities can be gradual, scattered rosettes of the quillworts making an occasional appearance in the *Myriophyllum* type of *Littorella-Lobelia* sward characteristic of deeper, stiller waters. *Littorella* and *Lobelia* can also extend some way, as a usually sparse cover, into the upper edges of the *Isoetes* stands, with *M. alterniflorum* and *J. bulbosus* remaining locally prominent too. The absolute depth of the switch from one vegetation type to the other varies somewhat with the amount of turbulence and the patterns are quite often complicated where there is any tendency to deposition of finer mineral material in the less turbulent waters below the more wave-disturbed area along the shore. Where this occurs, with banks of sand being laid down among stretches of gravel and boulders, stands of the *Utricularia* sub-community of *Juncus bulbosus* vegetation can occur among the *Isoetes* swards of moderately deep waters. Then, where richer silts accumulate in such places, there can be transitions to the *Potamogeton-M. alterniflorum* community (Figure 8). Boundaries tend to be quite sharp in these situations, but scattered quillworts can remain among the pondweed stands, and *Littorella* and *M. alterniflorum* are constant there, the latter often with high cover. Generally, though, *Potamogeton* spp. become much more prominent, with *P. perfoliatus*, *P. gramineus*, *P. berchtoldii*, *P. obtusifolius* and, in shallower waters, *P. pusillus* showing patchy abundance. Some kinds of floating-leaved aquatics can also root in these silted areas, notably *P. natans* and, more locally, *Nymphaea alba*, their foliage sometimes trailing out to form an open canopy over *Isoetes* stands in deeper water. Various patterns of these kinds can be seen in the vegetation maps from Cumbrian lakes in Pearsall (1918,

1921) and in the zonation diagrams of Spence (1964) from Scottish sites.

Greater diversity than this among aquatic assemblages in the same waters as *Isoetes* vegetation is generally limited to those lakes where there are sharp contrasts in shelter and substrates, as on opposed shores or where there is deposition around input streams, and even then there is limited contact between the quillwort stands and the more mesophytic communities. In more stable lake systems, the boundaries betwen the vegetation may remain fixed for very considerable periods of time but, if silting should transgress on to *Isoetes* vegetation, the quillwort plants are quickly overwhelmed because they cannot adjust their rooting level (Pearsall 1921). Then, with increased competition from other colonisers, the swards may be replaced by something like the *Potamogeton-M. alterniflorum*.

Even where substrates are less barren, much *Isoetes* vegetation occurs in waters too deep for direct invasion by emergents. In some places, however, the *Scirpetum lacustris* can be found sparsely represented among quillwort stands at moderate depth (Spence 1964) and, in stony shallows, transitions to *Littorella-Lobelia* vegetation may be locally complicated by the occurrence of the *Eleocharitetum palustris*. Where there is a shift to more peaty substrates in moderately deep waters, the *Caricetum rostratae* or *Equisetetum fluviatile* can be found inshore from *Isoetes* stands.

Distribution

Apart from a few far-flung stands in south-west England, this kind of vegetation is confined to north-west Britain.

Affinities

It has been customary in accounts of this vegetation from Britain (Pearsall 1918, 1921, Spence 1964) to separate off some kind of *Isoetes* community from *Littorella-Lobelia* swards and, although distinctions have to be made on dominance in transitional situations, this separation seems to make floristic and ecological sense. Indeed, with further sampling, it may be better to characterise two assemblages dominated by the different species of *Isoetes*. Such treatment conflicts with Continental approaches to this kind of vegetation which integrates it within a broadly-defined *Isoeto-Lobelietum* (Koch 1926) Tx. 1937 or its amendments (e.g. Schoof-van Pelt 1973). In whatever way these swards are defined, they clearly belong among the Littorelletalia communities grouped in what has been variously called the Isoetion (Ellenberg 1978), the Lobelion dortmannae Tüxen & Dierssen 1972 or the Littorellion Koch 1926.

Floristic table A23

Isoetes lacustris	V (4–10)
Myriophyllum alterniflorum	III (3–9)
Littorella uniflora	II (2–3)
Juncus bulbosus	II (1–5)
Potamogeton perfoliatus	II (1–6)
Nitella spp.	II (2–8)
Isoetes setacea	II (5–10)
Lobelia dortmanna	I (1–4)
Elodea canadensis	I (1–5)
Elodea nuttallii	I (1–7)
Sparganium angustifolium	I (1–3)
Potamogeton berchtoldii	I (1–6)
Potamogeton crispus	I (2–6)
Callitriche hamulata	I (1–3)
Potamogeton obtusifolius	I (1–2)
Callitriche hermaphroditica	I (1–2)
Chara spp.	I (1–4)
Subularia aquatica	I (4)
Scirpus fluitans	I (1–3)
Utricularia vulgaris	I (1–3)
Number of samples	37
Number of species/sample	3 (1–6)

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