Ecology of the Floating Water-plantain

Luronium natans

Conserving Natura 2000 Rivers

Ecology Series No. 9

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RV Lansdown & PM Wade

For more information on this document, contact:

English Nature
Northminster House
Peterborough
PE1 1UA
Tel: +44 (0) 1733 455100
Fax: +44 (0) 1733 455103

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Peterborough
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Conserving Natura 2000 Rivers

This account of the ecological requirements of the floating water-plantain (*Luronium natans*) has been produced as part of **Life in UK Rivers** – a project to develop methods for conserving the wildlife and habitats of rivers within the Natura 2000 network of protected European sites. The project's focus has been the conservation of rivers identified as Special Areas of Conservation (SACs) and of relevant habitats and species listed in annexes I and II of the European Union Directive on the Conservation of Natural Habitats and of Wild Fauna and Flora (92/43/EEC) (the Habitats Directive).

One of the main products is a set of reports collating the best available information on the ecological requirements of each species and habitat, while a complementary series contains advice on monitoring and assessment techniques. Each report has been compiled by ecologists who are studying these species and habitats in the UK, and has been subject to peer review, including scrutiny by a Technical Advisory Group established by the project partners. In the case of the monitoring techniques, further refinement has been accomplished by field-testing and by workshops involving experts and conservation practitioners.

Life in UK Rivers is very much a demonstration project, and although the reports have no official status in the implementation of the directive, they are intended as a helpful source of information for organisations trying to set 'conservation objectives' and to monitor for 'favourable conservation status' for these habitats and species. They can also be used to help assess plans and projects affecting Natura 2000 sites, as required by Article 6.3 of the directive.

As part of the project, conservation strategies have been produced for seven different SAC rivers in the UK. In these, you can see how the statutory conservation and environment agencies have developed objectives for the conservation of the habitats and species, and drawn up action plans with their local partners for achieving 'favourable conservation status'.

Understanding the ecological requirements of river plants and animals is a prerequisite for setting conservation objectives, and for generating conservation strategies for SAC rivers under Article 6.1 of the European Habitats Directive. Thus, the questions these ecology reports try to answer include:

- What water quality does the species need to survive and reproduce successfully?
- Are there other physical conditions, such as substrate or flow, that favour these species or cause them to decline?
- What is the extent of interdependence with other species for food or breeding success?

For each of the 13 riverine species and for the *Ranunculus* habitat, the project has also published tables setting out what can be considered as 'favourable condition' for attributes such as water quality and nutrient levels, flow conditions, river channel and riparian habitat, substrate, access for migratory fish, and level of disturbance. 'Favourable condition' is taken to be the status required of Annex I habitats and Annex II species on each Natura 2000 site to contribute adequately to 'favourable conservation status' across their natural range.

Titles in the Conserving Natura 2000 Rivers ecology and monitoring series are listed inside the back cover of this report, and copies of these, together with other project publications, are available via the project website: www.riverlife.org.uk.

Summary

The floating water-plantain (*Luronium natans* L Rafinesque) is an aquatic plant endemic to Europe. It has a complex life history and ecology and is notoriously difficult to identify. Consequently, it has been the subject of past misconceptions, notably regarding its distribution, ecological requirements and population dynamics. This report presents a review of all data available to the authors and clarifies many aspects of the plant's distribution, ecology and life history. Each topic is supported by informed discussion of data to support the conclusions reached, because some of these are in direct disagreement with accepted views.

The single most important conclusion is that the floating water-plantain has a number of apparently discrete reproductive strategies, defined here as: annual flowering, perennial flowering, and perennial vegetative. The second most important conclusion is that it occurs as dynamic metapopulations that contain different populations with different reproductive strategies. Any monitoring or conservation programme that does not take account of the dynamics of metapopulations and the requirements of the different reproductive strategies will not adequately represent the requirements of the species. Monitoring will provide a means by which data can be fed back into the system to refine conservation action. Further research is needed to explain the ecological requirements of some populations.

Richard Lansdown

The floating water-plantain has several reproductive strategies, each of which must be taken into consideration when monitoring or conservation programmes are initiated.

This review has shown that, based only on confirmed records, the range of the floating water-plantain extends from southern Norway and Sweden in the north, through the Republic of Ireland and France to northern Spain, east to Poland. Historically, it was found in the Czech Republic, but is now extinct. This is a much narrower range than has generally been accepted. Further survey work and a review of herbarium specimens are needed to confirm and enhance understanding of this range.

Conservation of the floating water-plantain must either ensure self-sustaining populations in wetlands or involve a long-term commitment to intrusive management. This report presents a guide to the setting of objectives for the conservation of the species in rivers and associated wetlands. However, the habitat in which a population occurs appears to be less important than other aspects of the ecology of the species. An appropriate research programme is suggested to provide further information necessary for the long-term conservation of the species.

Introduction

The floating water-plantain is an aquatic monocotyledon of the family Alismataceae. It is considered to be declining throughout its range. There have been several reviews of the ecology and/or conservation of the species, but none has provided information in a form that can be directly translated into conservation management or monitoring. This report presents a synthesis of data on the distribution, status and ecology of the floating water-plantain to serve as a baseline for further research and monitoring.

In most British reviews of the ecological requirements of the species there has been strong emphasis on data from the UK (Willby & Eaton 1993, English Nature in prep.). However, most remaining populations in the UK occur in upland lakes and canals, the majority of those in lowland habitats having been lost by the middle of the 20th Century. This may have led to an exaggerated emphasis on only a few aspects of the species' ecology.

Similarly, limited compilation of data from disparate sources outside the UK has led to a perception that populations of the floating water-plantain in Wales or in the canal systems of Britain are among its remaining strongholds (Willby & Eaton 1993; Kay *et al.* 1999; English Nature in prep.). This perception may not be accurate. Priority in this review was therefore given to a thorough collection of information from sources outside the UK to ensure that the conclusions reached could be applied to all facets of the species' ecology, distribution and population dynamics.

The aim of this review is to provide information on the ecological requirements of the floating water-plantain to inform the production of conservation objectives and monitoring protocols. The data reviewed include unpublished manuscripts on the distribution and status of the species throughout its range by a number of authors.

This report presents a guide to the setting of objectives for the conservation of the species in rivers and associated wetlands. However, the habitat in which a population occurs appears to be less important than other aspects of the species ecology. Therefore, conclusions are applied to conservation of *L. natans* in all situations, rather than specifically in rivers. A suite of attributes is established that may define favourable conservation status for the floating water-plantain. The basis for measurement of the degree to which these attributes are met is set out where possible as a series of quantifiable targets. Where available data are insufficient to set targets, this is highlighted and an appropriate research programme suggested to provide the necessary information.

The need for emphasis on the importance of population dynamics in the conservation of the floating water-plantain requires very precise use of terms. The following definitions have been employed:

- Site – a named area, with a defined boundary, supporting one or more populations of floating water plantain.
- Metapopulation – a group of populations connected by exchange of genetic material.
- Population – a discrete group of plants separated from other groups by an area of a habitat-type different to that supporting the floating water-plantain.
- Sub-population – a discrete group of plants separated from other groups by an area of habitat-type similar to that supporting the floating water-plantain.

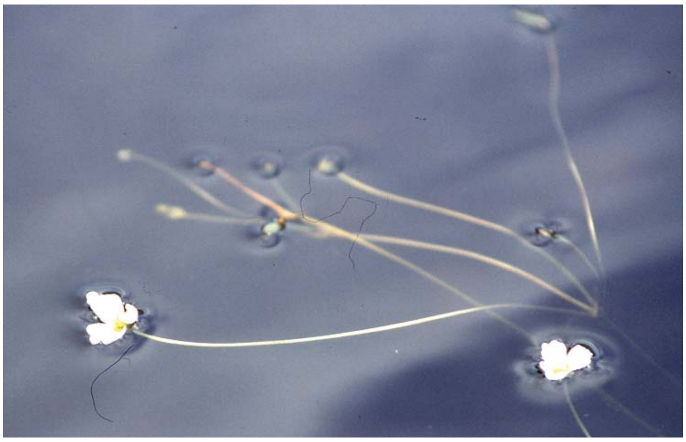
Distribution and status

Global range

The floating water-plantain is endemic to west and central Europe. The quality and coverage of data on its distribution and abundance varies throughout its range. The literature and a number of databases were reviewed, employing an approach described as 'high dispute tolerance' (IUCN 2001), which involves relying strictly on records that can be confirmed. Cook (1983) disregards records in Tutin *et al.* (1980) from Bulgaria, Italy and the former Yugoslavia. As a result of this review, the global range of *L. natans* has been revised. Based on confirmed records, its range can be described as extending from southern Norway and Sweden in the north, through the Republic of Ireland and France to northern Spain and east to Poland. It was also once found in the Czech Republic, but is now extinct.

It is most frequent in the western part of its range, in Britain (Kay *et al.* 1999); the Netherlands (Mennema *et al.* 1985); France (database of the Conservatoire Botanique National du Bassin Parisien); and northern Germany (Hanspach & Krausch 1987; Kaplan & Lenski 1989; Kaplan 1993). Outside this region it appears to be rare. Most accounts state that it is declining rapidly (Cook 1983). However, there are records from new sites from almost all countries in which it is still extant.

Both photos by Catherine Duigan/CCW



The only recent thorough survey of *L. natans* has been in Wales, where the floating water-plantain is found in sites such as Lake Bugeilyn (above and right).

The only area where there has been any thorough survey in recent years appears to be Wales, where 77% of historic sites still support populations (Kay & John 1995). It appears likely that the floating water-plantain is seriously under-recorded throughout much of its range. It is also possible that thorough survey in core areas may locate new populations and demonstrate that the decline, although real, is much less serious than has been stated as a result of the temporary colonisation of new sites.

UK distribution and status

In the UK, populations of the floating water-plantain considered native have been recorded from Glamorgan, Worcestershire and Northamptonshire, north to Anglesey, Argyll and Co. Durham. It also occurs as a small population, considered to have been deliberately introduced, in a single pond in the New Forest (Brewis *et al*. 1996). Similarly, populations in East Norfolk are considered to have originated as introductions (Driscoll 1985). It has never been recorded in Northern Ireland. Analysis of data from the UK is complicated by differences in methods of recording and presenting data.

Data held by the Threatened Plant Database (TPDB) (held by the Botanical Society of the British Isles) were subject to simple analysis. In this account, analysis has been based on 'named sites'. Thus, where a record is given against a site name that can be related to current site names, the record is recognised. Each named waterbody was recorded as a single site. Records were grouped by the first and last record as follows:

- Pre-1900 = only recorded before 1900.

- Pre-1900–1980 = recorded before 1900 and between 1900 and 1980.
- 1900–1980 = only recorded between 1900 and 1980.
- Pre-1900-present = recorded before 1900 and since 1980.
- 1900–present = recorded between 1900 and since 1980.
- Post-1980 = only recorded since 1980.

Analysis was restricted to records held on the TPDB as a single readily available source considered to be an up-to-date list of records. During preparation of this review, additional records have been reported from Cumbria (A Darwell, pers. comm.) and a detailed review of West Midlands records produced (Wade & Darwell 2000).

In the UK, the floating water-plantain has been reliably recorded in seven rivers and one stream. In three of the rivers there have been no records for many years: the Perry (last record 1924), the Roden (last record 1800), the Dee (last record 1948) and the Porthmelgan stream (last record 1944). It still occurs in four rivers: the Eden (in Snowdonia), Glaslyn, Gwyrfai and Teifi. There is also a recent record from the River Teme (1999) but this record must be considered unconfirmed.

England
The floating water-plantain has been lost from the majority of its recorded sites in England where, of a total of 67 named sites, only 16 are currently known to support populations. These losses have been almost throughout its range, with native populations recorded since 1980 only in Shropshire, Cheshire, south Lancashire, southwest Yorkshire, Cumberland, Northamptonshire and Staffordshire. Of these, only six are not in canals and are in what may be considered natural habitats.

Scotland
The distribution and history of floating water-plantain in Scotland is difficult to explain. It has been recorded from a total of eight sites in five vice counties. Of these, Wigtownshire, Ayrshire and South Aberdeenshire are all known to have supported populations at single sites, and all appear to have been lost. However, since 1980 a single population has been found in Fife, and a number of populations have been found in Main Argyll, none of which were known to support populations before 1980. Although no formal survey has been carried out in the area, there has been a general increase in surveys of aquatic plants in recent years.

Scottish populations of the floating water-plantain are mainly considered to be the result of introductions (NJ Willby pers. comm.) It has therefore been suggested that they should not be considered for conservation action, or that molecular analysis should be used to confirm their native or introduced status. However, given that they are sufficiently close to the natural range and in similar habitats to native populations, that they appear to function as dynamic metapopulations and are vulnerable, it would appear reasonable to treat these populations as an important resource even without information on their genetic relationship to known native populations.

Wales
A total of 48 named sites in Wales have been known to support populations of *L. natans*. It has been lost from 11 of these, but is still extant in 37. Of those lost, the most significant have been on Anglesey and in Glamorgan, where the floating water-plantain now appears to be extremely rare or extinct. There has been a reasonably thorough survey of Anglesey sites in recent years, and it appears likely that even the single post-1980 population has been lost due to habitat degradation and loss.

The most striking feature of the status of the species in Wales is that most (77%) populations are extant and 11 populations have only been known since 1980. This would imply that the species has not declined. However, there has been a series of systematic and relatively comprehensive surveys for the floating water-plantain, particularly in upland lakes, since 1990. This survey has confirmed the continued presence of plants in the majority of historically recorded upland Welsh sites and a number of new populations have been located.

Table 1. European distribution of *L. natans*.

	Total	Extant	% post 1950	
Belgium	?	3	100	Rare[1]
Czech Republic	1	0	-	Extinct[2]
Denmark		9	22	Nine current sites, increasing in artificial habitats[3, 4, 5]
France	?	?	?	Throughout except Mediterranean departments: locally abundant, locally declining, probably under-recorded[6-26]
Germany	455	179	?	Two main centres in the northwest and the east; significant decline, some colonisation of artificial habitats, possibly under-recorded, locally stable[27-39]
Ireland	?	2	50	May occur throughout much of the west coast, probably significantly under-recorded, status unknown[40]
Netherlands	299	123	44	Historically common, marked declines in certain areas, 299 squares before 1950 and 123 squares since 1950 of which at least 54 were new. Local decline, locally stable[41-43]
Norway	3	3	0	Three sites in one catchment, apparently increasing[44-45]
Poland	?	?	?	Historically not uncommon, more than half of historic sites may have been lost. Local decline, locally stable[46-47]
Spain	3	1	1	Two current sites, status unknown[48-50]
Sweden	4	2	100	Four of 25 provinces, currently two areas, one supports a number of populations. Apparently increasing[51-56]
United Kingdom	127	58	28	Local decline, locally stable/increasing (tables 2.3-2.5)
England	Lost from the majority of sites at which it has been recorded			
Scotland	Lost from two vice counties, but five new records since 1980			
Wales	48 sites, of these 77% currently support populations, maybe increasing but likely to be an artefact of comprehensive surveys and could have been in these sites for a long time.			

Data from different areas are not directly comparable, but are presented as an indication.
(References: [1]d'Hose & de Langhe 1977. [2]S Husak, pers. comm. [3]Mikkelsen 1943. [4]P Hartvig pers. comm. [5]Wind 1993. [6]Broyer *et al*. 1997. [7]Caussin 1907. [8]Clément, pers. comm. [9]Corillion 1981. [10]Danton & Baffray 1995. [11]Fournier 1961. [12]Greulich *et al*. in prep. [13]Haury 1985. [14]Haury 1988. [15]Haury & Muller 1991. [16]de Langhe *et al*. 1978. [17]Lansdown 2000. [18]Mériaux 1981. [19]Mériaux 1982. [20]Mériaux & Wattez 1981. [21]Netien 1993. [22]Poinsot 1972. [23]Provost 1993. [24]RV Lansdown unpubl. [25]Robbe 1984. [26]Saint-Lager 1883. [27]Benkert *et al*. 1996. [28]Casper & Krausch 1980. [29]Haeupler & Schönfeld 1989. [30]Hanspach & Krausch 1987. [31]Hegi 1981. [32]Kaplan 1992. Garve 1994. [33]Kaplan & Jagel 1997. [34]Kaplan & Lenski 1989. [35]Kaplan pers. comm. [36]Merkel 1982. [37]Oberdorfer 1970. [38]Philippi 1963. [39]Wittig & Pott 1982. [40]Rich *et al*. 1995. [41]Boerman 1975. [42]Mennema *et al*. 1985. [43]Van Ooststroom & Reichgelt 1964. [44]Holmboe 1930. [45]Lid 1952. [46]Boinski & Gugnacka-Fiedor 1988. [47]Zarzycki *et al*. 1992. [48]Amich & Elías Rivas 1984. [49]Perdigó 1983. [50]Rodriguez-Oubina & Ortiz 1991. [51]Aronsson *et al*. 1995. [52]Czeczott 1926. [53]Fritz 1988. [54]Hultén 1950. [55]Hultén 1971. [56]Mikkelsen 1943.)

Overview

Preparation of this report has resulted in a significant revision of the known global range of *L. natans*. This revision presents a much more discrete range that clearly shows the temperate-Atlantic affinities of the species. Information on the current status of the floating water-plantain throughout this range is summarised in Table 2.

Comparison of the 'total' and 'extant' columns gives the impression of a significant and alarming decline. However, the percentage of extant sites considered new since 1950 indicates an increase at least in some areas. Neither conclusion can be considered accurate, and the data available for this study are

Table 2. Conservation status of the floating water-plantain throughout its confirmed range.

Belgium	Rare	(ECE 1991)
Czech Republic	Extinct	(Š.Husák pers. comm.)
Denmark	Vulnerable	(P.Hartvig pers. comm.)
France	Vulnerable	(ECE 1991); nationally protected – Annexe I (Gaudillat in prep.)
Germany	Endangered	Red List 2 (Garve 1994)
Eire	–	
Netherlands	Vulnerable	Kwetsbaar (3); 50–74% decline (Van der Meijden *et al.* 2000)
Norway	Endangered	(ECE 1991)
Poland	Endangered	(Liro 1995)
Spain	Vulnerable	(ECE 1991)
Sweden	Endangered	(ECE 1991)
United Kingdom	Not threatened	Scarce (Stewart, Pearman & Preston 1994)

obviously inadequate to provide an accurate assessment of the species status. There are four main reasons for this:

- Difficulty in recognising the species.
- Difficulty in locating populations.
- Limited survey specifically for this species.
- Population dynamism, leading to an exaggerated perception of decline.

Detailed information on the distribution and abundance of the floating water-plantain is available from a few small areas, particularly parts of Germany and Wales. There is a lack of detailed, up-to-date information from Ireland, Poland and France that may all support globally important populations. These areas should be the subject of detailed survey and site data compilation.

Review of the international threatened status of the floating water-plantain (Appendix A), based on the revised IUCN criteria (Devillers *et al.* 1991), suggests that inclusion on the Global Red Data List is not justified using available data. However, the clear evidence for dramatic local declines in some areas, particularly within Germany and England, shows that the floating water-plantain is vulnerable and its inclusion on national or local Red Data Lists is justified.

The floating water-plantain is listed in annexes II and IV of the Habitats Directive and in Appendix 1 of the Berne Convention. It is not listed on the 1997 IUCN Red List of Threatened Plants (Walter & Gillet 1998) and holds no other formal international conservation status.

In some countries, sites have been notified under Natura 2000, at least partly for floating water-plantain populations. In the UK, the Cannock Extension Canal and Eryri in Snowdonia have been notified (Brown *et al.* 1997). In Denmark most sites for the floating water-plantain have been designated as Natura 2000 sites by the National Forest and Nature Agency, while two extant sites have been designated as EU-habitat areas selected partly on the basis of the occurrence of the species (P Hartvig pers. comm.).

Ecology

Molecular studies

There appear to have been few molecular studies of floating water-plantain, apart from a number of counts of chromosomes. The most significant study in terms of the conservation of the species involved isoenzyme analysis of a number of Welsh populations (Kay *et al.* 1999). Among the conclusions of this study are:

- The centre of genetic diversity in floating water-plantain populations in Wales lies in the upland pools and lakes around Llyn Teifi (and presumably in the River Teifi itself).
- Canal populations in the Welsh borders and West Midlands are likely to have derived from a single upland lake population.
- Populations in natural waterbodies are more genetically diverse than the populations in canals in the Welsh borders, even though the latter are larger.
- Possible deleterious effects of genetic erosion would be masked for long periods because it is likely that reproduction is principally vegetative and clones may survive for very long periods.

This highlights the importance of historic metapopulations relative to recent metapopulations. It also highlights the global importance of populations in the Welsh uplands, France and parts of Germany. Rivers are an uncommon habitat for this species in Britain (English Nature in prep.) but they are important in the context of genetic diversity (for example the Afon Teifi and associated waterbodies).

Growth form

Floating water-plantain is phenotypically very plastic. It is apparently stoloniferous, although what appear to be stolons are, in fact, modified inflorescence stems, which may be prostrate and creep through the substrate (Charlton 1973). Due to taxonomic issues, the stolons are often referred to as pseudostolons.

Two vegetative forms have been recognised according to leaf types (de Wit 1964):

- Form *submersum* (Gluck) with only submerged linear leaves.
- Form *repens* (Buch.) with expanded leaves.

However, the causes of variation in growth form are apparently environmental rather than genetic, and these forms are not consistent.

An understanding of some aspects of the morphology of the plant is fundamental to the survey and conservation of the species. The most important aspect of the growth form is that it can have two basic types of leaf. These have been referred to by a number of terms, particularly 'submerged' or 'floating'. However, the relationship between leaf shape and water surface is not consistent. It seems best to employ the term 'expanded', compared with 'linear-lanceolate', to reduce ambiguity.

In parts of its range, floating water-plantain can be mistaken for the following taxa, which can all have linear to slightly expanded basal leaves and stolons or procumbent stems:

- *Baldellia ranunculoides*, *B. alpestris*, *Limosella aquatica* (Jones & Rich 1998, Gaudillat in prep.).
- *Sagittaria* species (particularly the introduced *S. graminea* and *S. subulata*).

Both photos by Richard Lansdown

***L. natans* has two distinct forms: *submersum* (left), with linear leaves, and *repens* (right), with expanded leaves.**

Richard Lansdown

The floating water-plantain has stolons that may be up to 1 m long. Linear-lanceolate leaves are flat and only grow in water. Expanded leaves have petioles and blades, and may float or be submerged.

- *Sparganium* species, particularly young plants.
- *Alisma* species.

Richard Lansdown

***L. natans* can be confused with several other species, such as *Sagittaria graminea* var. *wetherbiana* (above). However, the flowers of *L. natans* are solitary, while those of *Sagittaria* spp. are borne on a compound inflorescence.**

Linear-lanceolate leaves

These translucent leaves number 20–100, each 2–4 mm, sessile, bifacial (flat in cross-section), tapering uniformly from a base about 4–7 mm wide to a fine acute (not obtuse) apex. They have a thicker green midrib occupying more or less the central half of the blade. Linear-lanceolate leaves are parallel-veined. In flowing water they may be parallel-sided, up to 50–60 cm long and 5–8 mm wide, and appear very different to those of plants growing in still water (Jones & Rich 1998). Linear-lanceolate leaves always grow submerged; they will not grow in air and wither if exposed by changing water levels. All linear-lanceolate leaves are basal, and *L. natans* can conform with the group of plants termed 'Isoetids' (Preston & Croft 1997). In certain circumstances, however, a series of plantlets arising along stolons can give the appearance of bunched leaves arising from a stem.

Expanded leaves

These leaves have petioles (stalks joining them to stems) up to 30 cm, and a blade 1–2.5 (maximum 4) cm x 1–3 cm (Sell & Murrell 1996). They are green, entire, ovate-oblong or elliptical, rounded or obtuse at apex, cordate (heart-shaped) to shortly cuneate (wedge-shaped) at base. Floating expanded leaves are coriaceous (leathery). Submerged expanded leaves may have translucent petioles up to 10 cm x 2 mm, obtuse at the apex, entire and yellowish green. Expanded leaves have a central vein, with a strong lateral vein either side of the midrib, to which they are connected by a series of smaller, weaker veins (Jones & Rich 1998). Floating leaves may be basal or may arise along ascending stems.

Stolons

Arising from the base of the rosette, stolons measure up to 1mm wide and may be more than 1m long (A Darwell pers. comm.). They are generally whitish, but are occasionally tinged green. They may be more or less prostrate and partly embedded in the substrate, or may rise toward the surface of the water.

Reproduction

L. natans has the potential to reproduce by a number of different means. Many populations flower well, and although there are few flowers at a time, they may be produced from June to August or September (RA Jones pers. comm.). Consequently, seed production can be high. However, there are other populations and conditions where flowers are rarely if ever produced, and in these cases reproduction is vegetative. Some populations produce self-fertilised flowers that remain submerged and do not open (cleistogamous) (A Darwell pers. comm.).

Flowers are solitary, or 2–5 in the axils of the leaves in simple umbels, with pedicels up to 7 cm. Stalked inflorescences are initially submerged, becoming floating. If submerged, they generally seem to be cleistogamous. Flowers typically arise in the axils of two of the bracts while a leafy shoot is developed in the axil of the third (Arber 1920). Bracts are small, ovate, acute at the apex and scarious. The three petals are 3.7–10 x 7–10mm, longer than sepals, subrotund or broadly obovoid, rounded at the apex, often with a wavy margin, white to more or less pale mauve with a yellow basal mark. The number of

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Up to 2 million seeds can be produced by flowering *L. natans*, such as this population with fruiting heads in the Brenne, France. Some populations, however, do not produce ripe fruit and so reproduce vegetatively, for example, in UK canals.

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The simple flower of *L. natans* is typical of plants served by generalist pollinators.

carpels per flower varies from 6–16 (Cook *et al.* 1974; Clapham *et al.* 1962; Ferguson 1991; Sell & Murrell 1996; Kay *et al.* 1999), to up to 25 (Rodriquez-Oubina & Ortiz 1991).

The simple cup- or bowl-shaped flower is typical of plants adapted for pollination by generalist pollinators, rather than through any specific mutualistic adaptation (Buchmann & Nabhan 1996). It is therefore unlikely that pollination is a constraint on populations. However, limited pollination may be the cause of very low seed-set in populations where only one or two flowers are open at any one time.

The means of reproduction is a fundamental consideration for conservation. Sexual reproduction allows for genetic exchange and maintenance or increase in the genetic diversity of populations. Vegetative reproduction is effectively clonal, and populations reproducing purely by vegetative means could be considered genetically identical. This can lead to inbreeding depression in populations through irreversible accumulation of deleterious mutations, an inability to adapt to biotic and abiotic changes, and an increase in viral load.

Dispersal

The floating water-plantain is well adapted to vegetative dispersal (Mikkelsen 1943) within hydrologically linked sites. Vegetative propagation and dispersal of shoots derived from the floral bracts is common and plentiful, while propagation by buds from roots and rhizomes is rarely observed. During the summer, large numbers of new individuals develop. These are initially connected by stolons, which, upon senescence, release new plants from the mother plant. Seedlings (Ridley 1930) and plants derived from senescent stolons float and readily disperse within a waterbody. This mode of distribution within and between sites is particularly important where floating water-plantain rarely or never flowers, and is likely to be an important factor in its spread within canal systems where plantlets may be carried by boat traffic (RA Jones pers. comm.).

Mikkelsen (1943) considers that the species is not particularly well adapted to dispersal by birds. However, Gaudillat (in prep) suggests that ingestion of seed by birds may be an important dispersal mechanism. This may be the most plausible explanation of how *L. natans* reaches new sites many kilometres from existing ones – for example, a new population that arose in a lake in southwest Sweden, 100 km from the nearest other site in the country (Fritz 1989). Similarly, a new population arose in a drainage canal in Lincolnshire, England, 50 km from the nearest known site (V Holt pers. comm.).

Life history

There is little detailed published information available on the life history of floating water-plantain. Individual plants may comprise a simple, linear-lanceolate leaf rosette, lacking stolons when young, or can have almost any combination of the features described above. Plants growing entirely exposed, for example on wet mud, will not have linear-lanceolate leaves. In all other circumstances, it is possible to have combinations of linear-lanceolate and expanded leaves, and submerged or emergent flowers. Similarly, plants growing in water more than a few centimetres deep may only have prostrate or procumbent stolons, or may have stolons rising toward the surface. Little is known about the factors influencing development of different features. It is possible for different subpopulations of a population to show different strategies.

Richard Lansdown

Local conditions, such as depth of water and light availability, can be determining factors in the growth form of *L. natans*. Unusually, the population above, growing in a forest ride, has emergent expanded leaves, probably because of the dense shade.

There appears to be a degree of consistency in the forms adopted by plants or populations and certain environmental conditions. These forms appear also to be consistently associated with methods of reproduction and consequently dispersal. The differences in reproductive potential and dispersal capacity of the different forms means that they must be treated differently in terms of monitoring and conservation management. The floating water-plantain is perennial, the perennating buds being found at or just below the surface of the sediment (Wade & Darwell 2000), although it can also function as a facultative annual (Szmeja & Clement 1990). For conservation purposes, the most important distinctions are between outbreeding and inbreeding, and between annual and perennial populations. As a basis for recording, populations can be simply defined as follows (though this definition may be modified as more data become available):

Perennial vegetative – submerged, linear-leaved

Typically, populations growing under 2 m or more of water with little seasonal variation in depth or in fast flow (Weeda *et al.* 1991) form extensive, closed carpets of linear-lanceolate-leaved rosettes. They appear not to flower, lack expanded leaves and rising stolons, but may have extensive prostrate stolons. These populations are perennial and, if they reproduce, this is exclusively through rhizome and root buds or stolons.

Perennial flowering – submerged and floating, linear and expanded leaved

Populations growing in relatively deep water with little seasonal variation in depth may form extensive, closed carpets of linear-lanceolate-leaved rosettes that may have submerged expanded leaves and floating leaves. They may produce small numbers of cleistogamous flowers and abundant floating flowers. They may have extensive prostrate stolons and often have abundant rising stolons with large numbers of plantlets formed per stolon. These plantlets often become detached from the stolons, and this is likely to be an effective means of dispersal within linked hydrological systems. It is also possible that plantlets are carried between hydrological systems by boats or even birds such as swans (*Cygnus* spp.). These populations therefore have potential for both sexual and vegetative reproduction.

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L. natans **sometimes grows in temporary waterbodies, such as the pond above, and can adapt its growth according to conditions. This population will perenate if the water remains, but function as an annual if the pond dries out.**

Annual flowering - terrestrial

Populations growing in temporary waterbodies may occur as open carpets of linear-lanceolate leaved rosettes in winter, but as the season progresses, they develop expanded leaves and eventually exist as open carpets of terrestrial plants, lacking linear-lanceolate leaves. These populations are obligately annual, as they cannot survive extended desiccation; they often flower abundantly and consequently dispersal is mainly by seed. These forms may also occur in the drawdown zones of permanent waterbodies.

An interesting feature of perennial vegetative populations is that annual flowering populations will form at intervals on the edge of the waterbody in which they occur. In large lakes, this often involves small stands in the wave-washed part of the margins or the drawdown zone. It appears likely that these derive from plantlets that become detached from stolons and are washed to the margin. This may represent a means by which populations that are normally limited to inbreeding by the depth of water can achieve outbreeding. If this is true, then the occurrence of these annual flowering populations may be fundamental to the long-term survival and genetic viability of perennial vegetative populations. There is a need for further research to confirm this.

Habitat

The floating water-plantain has been described as occurring in a remarkable variety of wetland habitats, including:

Natural standing water habitats

- Small ponds and pools in bogs, coastal areas, heathland and moorland, and dune slacks in both calcium-poor and calcium-rich areas (in the Netherlands).

- Larger still waterbodies: lakes, large moorland pools, oxbows and intermittently connected arms of large rivers.

Natural flowing water habitats:

- Slow-flowing rivers, streams (including fast-flowing streams).

Artificial waterbodies:

- Canals, ditches, reservoirs, balancing ponds, waterbodies created by mineral extraction and peat-diggings.

A comparison of habitats supporting *L. natans* suggests that it can occur in the majority of wetland types; in still water from small, temporary lowland pools to large, permanent, upland lakes, and in flowing water from small, fast-flowing streams to large sluggish rivers.

The list of wetland habitats from which it has been recorded therefore includes all but a very few types. It would therefore seem reasonable to conclude that habitat availability is rarely, if ever, a constraint on the distribution of *L. natans*. Habitat suitability is a different issue and will be considered below.

Edaphic factors

By their nature, environmental influences upon habitat are interlinked and the interactions complex. Thus, although the local geology of a waterbody may have a strong influence upon the pH and other chemical attributes, these are equally likely to be dictated by the chemistry of the catchment and of local drift.

Another factor rarely taken into account is that any one-off measure is a snapshot. Unless the 'health' of a plant or population can be measured, there is no guarantee that the plant is actually able to tolerate the conditions to which it is subject at the time of data collection. It has been shown that some aquatic macrophytes may take many years to respond to changes in water chemistry (J Bruinsma pers. comm.), although some changes may provoke a more rapid response. In the case of a slow response, if data are collected in the early part of the response of a plant to such a change, the evidence may suggest that the plant can tolerate the conditions, whereas given long-term surveillance this will be shown to be false.

Without rigorous testing, any conclusions reached on single measures, or even short-term surveillance data, must be employed with caution. The following accounts are taken directly from the literature with varying and often unspecified degrees of experimental support.

The floating water-plantain is often described as being typical of, or even an indicator of, acid water (Cook 1983, Weeda *et al*. 1991). However, it has been recorded from water with a wide range of pH values, from 3.6–6.1 (Arts *et al*. 1990a, Arts *et al*. 1990b), pH 5 (Smits *et al*. 1990 a, b), 5–6.5 (Szmeja & Clément 1990), and 5.8–7.2 (Hanspach & Krausch 1987). Similarly, the solid geology underlying populations varies from mildly acid (Libbert 1940), to circumneutral (Willby & Eaton 1993), mildly alkaline (Willby & Eaton 1993, J Bruinsma pers. comm. 2001) and even relatively base-rich (Willby & Eaton 1993, Greulich *et al*. 2000a), although the base status is not directly related to calcium content or alkalinity.

In a study in backwaters of the Rhône and Ain Rivers, a site supporting natural populations had a sediment pH of 7.0, while interstitial water had a pH of 7.4 (Greulich *et al*. 2000b). The Dombes fishponds, which support a number of populations, characteristically have naturally nutrient-poor sediment and are generally limed, resulting in an elevated pH of water with an average of 8 (range 7.1–9.4) (Broyer *et al*. 1997). Although disputed by Cook (1983), *L. natans* has been shown to tolerate calcium (Greulich *et al*. 2000b).

Tolerance of a range of pH values from 3.6–8 would suggest that acidity is not a determining factor in habitat suitability for floating water-plantain. A number of authors have noted that acidification of waterbodies can lead to a decline and eventual loss of populations (Plate 1985). Schaminee *et al*. (1995) suggest that a decline in pH from 5.5 to 4.4 can result in loss of stands of the Littorelletalia. However, experimental studies have shown that plants can remain viable in culture solutions as acid as pH 4 (Maessen *et al*. 1992).

L. natans is associated with a number of soil types, including sand (Van Ooststrom *et al*. 1964; Smits *et al*. 1990a; Arts & den Hartog 1990a), sand with gravel (Arts & den Hartog 1990a), silt (Arts & den Hartog 1990a) and peat (Van Ooststrom *et al*. 1964, Weeda *et al*. 1991). However, an important factor appears to be an absence of layers of deep organic sediment (Schaminee *et al*.1995, J Bruinsma pers. comm. 2001).

The floating water-plantain is often described as being characteristic of oligotrophic waters (Fritz 1989, Willby & Eaton 1993; Lockton & Whild 1995; van den Munckhoff 2000). However, it is also recorded from meso-oligotrophic (Mériaux & Wattez 1981; Cook 1983; Arts & den Hartog 1990a), mesotrophic and meso-eutrophic (J Bruinsma pers. comm. 2001) to eutrophic waters (Willby & Eaton 1993).

Similarly, it has been described as occurring on moderately nutrient-rich soils (Arts & Den Hartog 1990, Smits *et al*. 1990a). There are also claims that it does not occur in polluted water (Mennema *et al*. 1985). In the south of the Netherlands *L. natans* appears to have its most important strongholds in regions with iron-rich seepage, and it has been described as being limited to nutrient- and phosphate-poor waters (van den Munckhoff 2000). Conversely, in Denmark, Mikkelsen (1943) considered the species to require relatively nutrient-rich conditions, hence its presence in the River Vorgod and in the mouth of the River Skjern. This view is also put forward by Køie (1944) describing the occurrence of *L. natans* in the River Skjern.

The main conclusion that can be reached from the literature is that floating water-plantain appears to have a very wide range of chemical and substrate tolerances. However, accounts are often conflicting and the only way to clarify these issues is through reasonably long-term experimental study. If all the above statements are accepted, then it would appear unlikely that these parameters can be regarded as limiting distribution or abundance. However, the level of disagreement suggests that they should be treated with caution.

Phytosociology

Several studies of the geographical associations of European plants have included floating-water plantain. Most class this species in one of the Atlantic groups (Arts & den Hartog 1990a), either in an Atlantic (Haury *et al*. 1994) or a Sub-atlantic (Czeczott 1926) subgroup. In a somewhat different classification, it has also been assigned to a Suboceanic Temperate group of species (Preston & Hill 1997). Revision of the range of the species appears to indicate that it has a stronger Atlantic association (Preston & Hill 1997) than is implied by the definition of Suboceanic Temperate (Preston & Hill 1997).

Cook (1983) describes it as occurring in the *Isoeto-Lobelium* and the *Littorello-Eleocharitetum*, but also in the *Myriophyllo-Nupharetum* and in some *Nymphaea*-dominated associations. Most other accounts place floating water-plantain in the Littorellion or Littorelletea (Ellenberg 1963) communities (for example, Schaminee *et al.* 1995). The National Vegetation Classification (Rodwell 1995) lists floating water-plantain as associated with A11, the *Potamogeton pectinatus-Myriophyllum spicatum* community. However, this does not conform well with other data on its phytosociology and may be an artefact of recording methods.

Other wetland species assigned to the same classes include *Deschampsia setacea* (Arts & den Hartog 1990a); *Eleocharis multicaulis* (Arts & den Hartog 1990a, Preston & Hill 1997); *Eleogiton fluitans* (Arts & den Hartog 1990a); *Littorella uniflora* (Preston & Hill 1997); *Pilularia globulifera* (Arts & den Hartog 1990a; Czeczott 1926; Preston & Hill 1997); and *Potamogeton polygonifolius* (Arts & den Hartog 1990a, Preston & Hill 1997). In addition, *Apium inundatum* (Preston & Hill 1997, Arts & den Hartog 1990a), *Baldellia ranunculoides* (Czeczott 1926, Arts & den Hartog 1990a) and *Elatine hexandra* (Czeczott 1926, Arts & den Hartog 1990a) are assigned to the same classes, but with different sub-group affinities. Most of these species have, at some time, been recorded with *L. natans* (see below).

It is notable that many of the species included within the classes to which floating water-plantain is assigned also have an association with temporary pools – for example, *Apium inundatum*, *Baldellia* *ranunculoides*, *Deschampsia setacea*, *Elatine hexandra*, *Eleogiton fluitans*, *Littorella uniflora* and *Pilularia globulifera*. Most of these are also considered to be declining throughout much of their range.

Associated species

The different habitat-types and relatively discrete growth-forms complicate characterisation of species associated with floating water-plantain. Most studies have simply addressed the taxa recorded in the same waterbodies, describing plants as associated without defining the nature of the association or even recording plants within a specified distance of stands of *L. natans*. In addition, rarely, if ever, has any distinction been made between plants occurring with floating water-plantain and the growth form represented. However, a review of the taxa described as associated clearly shows that not all habitats will support the same species. For example, it is unlikely that *Elatine alsinastrum*, a species typical of the draw-down zones of lakes, will occur in close proximity to *Nitella* or *Cladophora* species, which cannot tolerate exposure to the air.

An understanding of associated species is one of the better means of indicating habitat affiliations and is fundamental to most of the habitat classification systems used in conservation. However, only very rarely is information collected that enables an identification of the association referred to. In many cases, it is not possible to collect data based on a recognized association. In these cases, data should be recorded from within a specified distance of the plant. Ideally, plant species should be recorded in bands around a stand at set distances. This enables an understanding of whether plants are simply occurring in similar conditions, or whether there is indeed an association.

A large number of species have been recorded as associated with the floating water-plantain. As is to be expected, most have been reported only once. The following have been reported more than once:

- *Alisma plantago-aquatica* (Rodriquez-Oubiña & Ortiz 1991, Broyer *et al*. 1997, Lansdown 2000).
- *Apium inundatum* (Bournérias 1979; Rodriquez-Oubiña & Ortiz 1991; Weeda *et al*. 1991, Haury *et al*. 1994; Haury 1996; Lansdown 2000; RA Jones pers. comm.).
- *Baldellia ranunculoides* (Rodriquez-Oubiña & Ortiz 1991, Weeda *et al*. 1991).
- *Eleocharis acicularis* (van Ooststroom *et al*. 1964; Hanspach 1991; Weeda *et al*. 1991; Haury 1996; Broyer *et al*. 1997; Lansdown 2000).
- *Eleocharis multicaulis* (Rodriquez-Oubiña & Ortiz 1991, Kaplan 1993).

Both photos by Richard Lansdown

The floating water-plantain is often associated with pond water-crowfoot (*Ranunculus peltatus*) (top) and broad-leaved pondweed (*Potamogeton natans*) (bottom).

Both photos by Richard Lansdown

***L. natans* is often associated with floating clubrush (*Eleogiton fluitans*) (top) and needle spike rush (*Eleogiton acicularis*) (bottom).**

- *Eleocharis palustris* (Rodriquez-Oubiña & Ortiz 1991; Haury 1996; Lansdown 2000).
- *Eleogiton fluitans* (van Ooststroom *et al.* 1964; Weeda *et al.* 1991; Kaplan 1993).
- *Elodea canadensis* (Hanspach 1991, Greulich *et al.* 2000a).
- *Elodea nuttallii* (Haury *et al.* 1994, Greulich *et al.* 2000a).
- *Glyceria fluitans* (Hanspach 1991, RA Jones pers. comm.).
- *Hypericum elodes* (Weeda *et al.* 1991; Kaplan 1993; RA Jones pers. comm.).
- *Juncus bulbosus* (Hanspach 1991; Rodriquez-Oubiña & Ortiz 1991; Kaplan 1993; RA Jones pers. comm.).
- *Littorella uniflora* (Rodriquez-Oubiña & Ortiz 1991; Kaplan 1993; Haury 1996; J Bruinsma pers. comm.; RA Jones pers. comm.).
- *Lythrum portula* (Lansdown 2000, RA Jones pers. comm.).
- *Potamogeton natans* (Balocco-Castella 1988; Hanspach 1991; Weeda *et al.* 1991).
- *Potamogeton polygonifolius* (Hanspach 1991; Rodriquez-Oubiña & Ortiz 1991; Weeda *et al.* 1991; Haury *et al.* 1994; Lansdown 2000; RA Jones pers. comm.).
- *Ranunculus peltatus* (Haury *et al.* 1994; Haury 1996; Lansdown 2000).
- *Sparganium natans* (van Ooststroom *et al.* 1964; Lansdown 2000).

These species can be split into three simplistic groups:

- Species generally associated with ephemeral waterbodies: *Apium inundatum, Baldellia ranunculoides, Eleocharis multicaulis, Glyceria fluitans, Juncus bulbosus, Littorella uniflora* and *Lythrum portula*.
- Species associated with permanent waterbodies: *Elodea canadensis, E.nuttallii, Potamogeton natans, P. polygonifolius, Ranunculus peltatus* and *Sparganium natans*.
- Species with no such strong association: *Alisma plantago-aquatica, Eleocharis acicularis, E. palustris, Eleogiton fluitans and Hypericum elodes*.

These hydroperiod associations are not exclusive, and it is even possible that floating water-plantain may occur with a species such as *Ranunculus peltatus* when a waterbody is inundated, and with terrestrial species when the same waterbody is dry. In fact, a perceived community can change dramatically and rapidly from predominantly aquatic to predominantly terrestrial within a single season. These factors must be taken into account when recording the phytosociological associations of the floating water-plantain.

Limiting factors and causes of decline

L. natans has been shown to be intolerant of competition (Willby & Eaton 1993, Greulich *et al.* 2000b).

The cause of this intolerance is not yet clear, but there are three possible causes:

- Physical suppression.
- Competition for light or nutrients.
- Chemical suppression (such as allelotoxins).

Competition and succession are probably major influences limiting the distribution and abundance of the floating water-plantain, which must, to some extent, depend upon factors suppressing colonisation by more aggressive plant species. These factors will operate in different ways in relation to the various growth and reproductive strategies of *L. natans*.

In temporary waterbodies, where populations are annual and reproduce through outbreeding, the main process suppressing colonisation by aggressive plants is consolidation of the substrate during drying. This is also the process by which temporary ponds remain a permanent feature of the landscape (P Williams pers. comm.). Poaching by grazing animals is another factor suppressing the development of more established vegetation.

In permanent, shallow, lowland meso-eutrophic waterbodies, there are few processes that will suppress succession. In larger waterbodies wave action is certainly an important factor, and if connected to a river, scour may have a similar effect. However, it is notable that in part of the Vieux Rhône, floating water-plantain disappeared in 1991 after floods of exceptional intensity (Henry *et al*. 1996). This may have been linked to lowering of groundwater levels after major incision of the Rhône riverbed caused by gravel extraction (Bornette & Heiler 1994). Where the species is able to develop a dense floating leaf canopy, its competitive ability may be enhanced (Greulich *et al*. 2001).

In permanent, deep or upland, meso-oligotrophic or oligotrophic waterbodies, the main factors appear to be lack of light at depth, wave action and poor nutrient status. It is also possible that colonisation by an alien species, such as swamp stonecrop (*Crassula helmsii*) or floating pennywort (*Hydrocotyle ranunculoides)*, could pose a threat.

In many sites that currently support the floating water-plantain, factors suppressing succession are artificial and include disturbance of sediment by light boat traffic (Willby & Eaton 1993) and dredging (Hanspach & Krausch 1987, Willby & Eaton 1993).

The species involved in succession will depend upon habitat. Thus, for example in lowland heathland pools, succession will generally be characterised by grasses such as *Agrostis stolonifera* or the small *Glyceria* species, or by taller coarse grasses such as *Deschampsia cespitosa*. However, it has been shown that acidification of small heathland or bog pools leads to a loss of the *Littorelletea* communities through succession to *Sphagnum-Juncus bulbosus*-dominated vegetation (Dierssen 1981; Roelofs 1983; Weeda *et al*. 1991; Kaplan 1993; Wittig 1995; Roelofs *et al* 1996; Wittig 1996).

In larger, lowland mesotrophic or eutrophic waterbodies, typical species will include *Carex elata, C.rostrata, Glyceria maxima, Phalaris arundinacea, Phragmites australis* (Dierssen 1981, Kaplan 1993), *Sparganium emersum* (Greulich *et al*. 2001) and *Typha latifolia* (Dierssen 1981, Kaplan 1993). In these conditions, natural processes of nutrient enrichment may be exacerbated by eutrophication from agriculture (Dierssen 1981; Mériaux 1981; Wittig & Potts 1982; Plate 1985; Schaminée *et al*. 1992; Kaplan 1993). In upland and other oligotrophic waterbodies, if succession occurs it appears to be often associated with an anthropogenic change in nutrient status or water acidity and similar species to those involved in the lowlands.

Another possible cause of loss could involve the spread of invasive alien aquatic plants. While this has not yet been proven, the spread of *Crassula helmsii* in the British Lake District is encroaching upon *L. natans* populations, and it is unlikely that the latter will be able to compete (A Darwell pers. comm.).

It is notable that: "The principle threat in Britain is now from restoration of waterways and the expansion of recreational boating, while acidification of upland lakes represents a remote but potentially significant long-term risk" (English Nature in prep.).

Both photos by Richard Lansdown

Small *Gyceria* species such as *G. fluitans* (top), and *Carex rostrata* (bottom) can be a threat to *L. natans*.

Population dynamics

Throughout the whole of its range, the floating water-plantain is described as declining. It is clear that there have been losses in some regions where there have been reasonably comprehensive surveys of sites over the last hundred years, such as the West Midlands of the UK (Wade & Darwell 2000). Here, most suitable habitat and many sites have been lost, and there is only very localised potential for the species to survive. However, the review of distribution and abundance data suggests that the decline may be concentrated in a number of relatively discrete areas. Elsewhere, although there have been some losses, new populations are also being discovered.

In most cases where suitable data are available, it is clear that in any area, a high proportion of sites will have records of *L. natans* for a single year (Wade & Darwell 2000, Kay *et al.* 1999). The remainder may have a discontinuous history of records over hundreds of years. This would suggest that many records represent failed colonisation of new or temporary sites. It is likely that the few sites with stable populations act as inocula for dispersal to suitable habitat as it becomes available. This makes them particularly important as a focus for conservation effort.

Tables 3 and 4 show summaries of data from the Threatened Plant Database (TPDB) and the database of the Conservatoire Botanique National du Bassin Parisien (CBNBP). This analysis shows that simply listing presence or absence from a site is not a reasonable indication of the status of this species. It is clear that, although the species may disappear from one site, it is just as likely to be found at a new site. The main points that can be derived from this analysis are:

- Fifty-seven (46%) of a total of 124 historic sites in Britain still support *L. natans*, of these 21 (37%) are considered new since 1980.
- Thirty (24%) of a total of 127 sites in the Parisian Basin still support *L. natans*, of these, 28 (93%) are considered new since 1980.

Therefore, 22% of all known sites in the Parisian Basin and 17% of all known sites in the UK support populations found since 1980.

A similar picture can be seen in the Netherlands. Of the 123 squares from which it has been recorded since 1950, at least 54 (44%) were from new squares (Mennema *et al.* 1985). In Wales, the only area where there has been any thorough survey in recent years, 77% of historic sites still support populations and at 23% of sites it was first recorded after 1980.

The remarkable populations of floating water-plantain found in the Montgomery Canal have provoked controversy. Some authors suggested that the plant was actually increasing and that it should not be a cause for concern. However, others regarded this as a spread into 'artificial habitats' while the species declined or disappeared from 'natural habitats'.

Similar colonisation of newly created habitats has been reported from Denmark (P Wind pers. comm.),

Table 3. Summary of British records (source: TPDB).

1740–1900	**1740–1980**	**1900–1980**	**1740–post 1980**	**1900–post-1980**	**1980 onwards**
24 (19%)	4 (3%)	39 (32%)	14 (11%)	22 (18%)	21 (17%)
No. of sites where *L. natans* no longer occurs			**No. of sites supporting *L. natans* since 1980**		
67 (54%)			57 (46%)		

Table 4. Summary of records from the Parisian Basin (source: CBNBP).

1740–1900	**1740–1980**	**1900–1980**	**1740–post-1980**	**1900–post-1980**	**1980 onwards**
86 (68%)	1 (1%)	10 (8%)	1 (1%)	1 (1%)	28 (22%)
No. of sites where *L. natans* no longer occurs			**No. of sites supporting *L. natans* since 1980**		
97 (76%)			30 (24%)		

Germany (Hanspach & Krausch 1987) and Sweden (O Fritz pers. com.). In the late 1960s the estuary of the river Skjern in Denmark was regulated, resulting in the construction of the Søndre Parallelkanal, which was colonised by *L. natans*. It seems to have spread rapidly to suitable sites over the last 10 years, presumably due to improved connectivity and water quality, especially in the river Skjern and its tributaries. It is also notable that floating water-plantain was not recorded in Norway or Sweden until the 20th Century.

The accounts and analysis described here enable a number of conclusions to be reached about the dynamics of populations:

- Populations are capable of persisting at a single site for hundreds of years.
- The species has been lost from more than 50% of known sites in the two main regions for which data were analysed.
- Of the sites where it still occurs, 37% of British sites and 93% of sites in the Parisian Basin were found since 1980.
- It is capable of colonising sites that are either already suitable or become suitable later.
- Some new sites may be historic oversights.

At Brown Moss in Shropshire, *L. natans* was recorded regularly from 1955 to 1987 (TPDB 2001). There was then a period of 12 years during which surveys based mainly on the shoreline and shallow water resulted in no confirmed records (TPDB 2001). The conclusion was reached that the species was extinct at the site (S Whild pers. comm. 1998). However a population was located in a well-surveyed pool in 1999 (Wade & Darwell 2000). These records suggest that in some circumstances *L. natans* may not grow at a site in every year, but may have some means of dormancy. A similar picture is gained from Dowrog Common in Pembrokeshire, where, after fairly regular records, a detailed survey carried out in the early 1980s found no *L. natans*. After the pond was scraped in 1986–1987, floating water-plantain was recorded in 1996 (RA Jones pers. comm.). This would suggest that the species has a capacity for extended dormancy (up to 12 or 16 years). This cannot be confirmed, as it is not possible to be certain that populations were not missed in the years with no records or that *L. natans* did not colonise from an unknown neighbouring site.

Most lowland populations of the species are likely to be parts of dynamic metapopulations, developing and declining in response to natural and anthropogenic changes in habitat suitability. The main cause of decline in these populations in recent years is through direct habitat loss, where waterbodies have been drained for development or conversion to agriculture. Additional losses have occurred in remaining sites through acidification and eutrophication. Populations in deep upland and other oligotrophic lakes are likely to be stable unless they are subject to acidification or eutrophication. This is borne out by data from the UK, where populations throughout most of England have been eliminated through direct habitat loss, although there may also have been losses through pollution.

All these factors suggest that in lowland and mesotrophic or eutrophic waterbodies, *L. natans* functions as a series of dynamic metapopulations where, although it will be lost from some sites, it will persist at others and will also colonise new sites. Moreover, even at sites where it persists, it will not necessarily occur every year. One of the most striking features of plants with dynamic metapopulations is that when site data are mapped with symbols separating records from specified cut-off dates (Preston & Croft 1997, Stewart *et al.* 1994), they can only show a decline, unless the species is still present at all sites where it has ever occurred. In the case of *L. natans*, this will be exacerbated by the large number of sites involving failed or short-term colonisation.

It is clear that protection of a single lowland waterbody will be ineffectual for conservation of *L. natans*. In all cases, except possibly those involving perennial vegetative populations, it will be necessary to protect the complexes of wetlands and processes that support metapopulations.

Management and conservation

There has been little active conservation management specifically for the floating water-plantain. In the UK management of some canal systems has obviously been important for the survival of many populations (Willby & Eaton 1993). However, no detailed data are available on the management actions or their consequences. An attempt has been made to transplant populations into series of off-line reserves along the Montgomery Canal, to guard against loss due to increased boat traffic and upgrading (Briggs 1988). However most of these have been unsuccessful and transplanted populations have died out (RV Lansdown unpublished).

Information is presented here on two areas in which there has been work aimed at this species or communities in which this species occurs. Additional information is provided on traditional management practices that favour the species in regions of France and Germany.

Dowrog Pool, Pembrokeshire, southwest Wales
L. natans was first recorded from Dowrog Common in 1905 (Appendix A). Subsequently, there were sporadic records between 1925 and 1936 and a single record in 1963. The area was searched in the early 1980s and no *L. natans* found. The pool was very overgrown, with little or no open water (RA Jones pers. comm.). Between 1985 and 1987, part of the historic pool was scraped to create an area of open water and to attempt recovery of populations. A vegetative rosette of *L. natans* was found in 1996 and the species subsequently formed a reasonably large population.

The scrape is shallow and dries out in summer. Throughout the year it supports dense stands of other vegetation, dominated by *Potamogeton gramineus*. It appears likely that in the relatively near future, the pool will again have to be scraped to reduce competition if the aim is to maintain a growing population. Thus, although apparently successful, maintenance of a healthy population is likely to be dependent upon an intrusive and fairly onerous management regime.

The Netherlands
There have been several interventions with the aim of restoring stands of *Littorelletea* communities (Roelofs *et al.* 1984; Weeda *et al.* 1991; Schaminée *et al.* 1995; Roelofs *et al.* 1996) using a variety of approaches.

Habitat creation by scraping or excavating sites has been successful where the community is in severe decline or extinct. However, in small and shallow excavations, succession may be very rapid and may lead to a requirement for an intensive management regime, similar to the approach on Dowrog Common. In larger excavations, processes such as wave action will suppress colonisation by dense aquatic plant communities, while over 0.5m depth, macrophyte communities will become still more limited. Generally, these excavations should have gently sloping sides to enable colonisation of the draw-down zone. However, inclusion of lengths of shoreline with a steeper slope will locally reduce build up of detritus. Excavation in sites suffering acidification will not be effective in the long-term, unless some means of combating or buffering acidity is employed (Schaminée *et al.* 1995).

Mowing and removing plants at and near the shore may reduce eutrophication and may suppress colonisation by dense aquatic macrophyte communities, but it involves an intensive management commitment. It is also important to note that 'in shallow lakes, aquatic plants may serve to hoard large populations of *Cladocera* which move out at night to graze or which graze on phytoplankton in water moved by wind through the plant bed' (Moss 1995). In this way, beds of aquatic plants are important for zooplankton, which can reduce phytoplankton populations and improve light quality.

Manipulation of water-levels (for example for ice rinks), imposing artificially low summer levels and high winter levels, can suppress colonisation and therefore slow succession. However, it appears to have a low level of success in sites with poor water quality.

Grazing may be effective, particularly where *L. natans* occurs as an annual in temporary waterbodies, but there is a risk of eutrophication from manuring and excessive poaching as the waterbodies dry out in the summer. It should be noted that this form of poaching may be the main means of dispersal for species such as *Ranunculus tripartitus* (Lansdown & Evans 2001) and *Tolypella intricata* (Lansdown & Stewart 1999) which share elements of the dispersal strategies of *L. natans*.

Two further examples also provide an insight into potential conservation management techniques:

The Dombes fish-ponds to the northeast of Lyon, which support a number of populations of floating water-plantain, are managed on a system that involves fish-farming for two years, followed by drainage and production of a cereal crop for a year. This system dates from at least the 13th Century. Inundation introduces organic matter, while the subsequent drainage enhances aeration and mineralisation of the soil and control of parasites (Broyer *et al*. 1997). This system is employed, generally with drainage but without cereal production, throughout much of continental Europe, including other parts of France such as the Sologne (P Jauzein pers. comm.), Belgium (J Bruinsma pers. comm.) and the Czech Republic (Š Husak pers. comm.). The system is no longer used in the UK, but a crop was grown at Fowlmere in Breckland in the past, when water levels were naturally particularly low (B Nicholls pers. comm.) and historically, fish ponds near Runnymede were drained at intervals (F Rumsey pers. comm.). This practice almost certainly suppresses colonisation by large grasses and most other aggressive aquatic plants, while favouring species that can grow both as deep water aquatics and on exposed mud.

Within the 'Schraden', the eastern centre of abundance of the floating water-plantain in Germany, ditches supporting the species have been subject to an annual weed-cut once a year for more than 100 years, and sediment is dredged once every three years (Hanspach & Krausch 1987). The stability of populations in the Schraden seems to be due to the particular ditch management system. Regular removal of vegetation and organic sediment creates open areas that can be colonised by pioneer species like floating water-plantain (Hanspach & Krausch 1987). It is also likely that the surviving naturally oligotrophic

Both photos by Richard Lansdown

***L. natans* can grow in a variety of conditions, such as in a forest stream (above, in the foreground), and on the edge of a fish farm basin (bottom).**

Photos by Richard Lansdown

The Dombe fish farm system. Top: a fully inundated basin in which carp are raised. Centre: drained basin with a cereal crop and the remains of a ditch. *L. natans* is growing at the edge of the water. Bottom: a basin partially reinundated following harvest, with the white flowers of *Ranunculus aquatilis* showing furrows.

sections function as refugia from which the species can colonise suitable habitat as it becomes available.

There is no available information on management of upland lakes for floating water-plantain. However, recent surveys in Wales have shown that these populations are amongst the most stable and it appears unlikely that management will be needed unless there is a change in the water chemistry or processes suppressing succession. Management of lowland habitats specifically for the species is likely to require frequent intrusive intervention, such as scraping or dredging. Liming of upland catchments has not been shown to affect floating water-plantain, and given the range of pH data and substrate affinities recorded, it appears unlikely that it will have any significant affect.

It is clear that conservation management of floating water-plantain cannot simply be approached as a single standard for the species. The different growth forms and reproductive strategies are subject to different types of threat, which must be dealt with in different ways. In addition, the different context in which these populations grow will be subject to different types of threat, for which a suite of responses must be available.

Table 5 illustrates a very basic approach to assessment of the need for appropriate management in different circumstances. This table could be seen as forming the baseline for management decisions linked to a monitoring program. However, it will not be effective unless monitoring is iterative, allowing feedback of data and information gained through experience into the decision-making process.

Conclusions

The floating water-plantain can grow in a variety of forms and conditions. These different growth forms are intimately linked to the reproductive strategy of populations and environmental conditions, and may dictate different conservation actions. The growth forms can be simply classed as follows:

- Perennial vegetative populations and many perennial flowering populations of *L. natans* occur as persistent, largely stable populations in deep water. Perennial flowering populations in naturally meso-eutrophic habitats are likely to be dynamic and very vulnerable.
- Annual flowering populations of *L. natans* occur as dynamic metapopulations, where individual populations will colonise, expand and set seed in suitable habitat and then decline and disappear due to community succession. These populations tend to be prevalent in lowland heathland and are the most severely threatened by habitat loss, acidification and conversion of land to agriculture, as they are reliant upon dynamic complexes of temporary waterbodies.

Table 5. Management decision breakdown.

Annual flowering	Succession	Change in balance of cover of *L .natans*, bare substrate and other vegetation	Identify cause of change if possible. Succession is a natural element of the dynamism of some populations and no response may be appropriate if the metapopulation is in favourable condition. Possible actions include dredging and weed-cutting.
	Acidification	Change in balance of species, involving relative or actual increase in taxa such as *Sphagnum* and *Juncus bulbosus*	Limited information available. Control at source is unlikely to be an option. Possible actions include creation of new, pH buffered scrapes (e.g. liming). pH buffering in sites supporting *L . natans* may not be advisable.
	Eutrophication	Colonisation by taxa such as large *Juncus* spp. and coarse grasses	Identify nutrient source and assess whether input can be deflected or treated. If this is not an option, assess potential to establish new habitat to allow the establishment of replacement populations.
Perennial flowering	Succession	Change in balance of cover of *L. natans*, bare substrate and other vegetation, particularly stand-forming species such as *Sparganium erectum* and coarse grasses	Identify cause of change if possible. Succession is a natural element of the dynamism of most perennial flowering populations and no response may be relevant if the metapopulation is in favourable condition. If a response is deemed appropriate, this should involve restoration of a self-maintaining system. If this is not possible, then dredging or weed-cutting may be necessary.
	Eutrophication	Decline in relative cover of *L .natans*, increase in relative abundance of taxa such as tall monocotyledons and algae.	Identify nutrient source and assess whether input can be deflected or treated. If this is not an option, then artificial removal of vegetation may be necessary.
Perennial vegetative	Succession	Change in balance of cover of *L. natans*, bare substrate and other vegetation, particularly species such as *Crassula helmsii* and *Elodea* spp.	No information

L. natans can occur in the majority of wetland types, in still water from small, temporary lowland pools to large, permanent, upland lakes, and in flowing water from small, fast-flowing streams to large sluggish rivers. It would therefore seem reasonable to conclude that habitat availability per se is rarely, if ever, a constraint on the distribution of *L. natans*.

Rivers are likely to support all the growth-forms and strategies recorded in different situations, particularly if associated waterbodies (headwater and oxbow lakes) within the catchment are included.

The survival of floating water-plantain populations is primarily dependent upon factors suppressing community succession. In many lowland areas, traditional management of fish ponds or ditch complexes fulfills this role. Sites where natural processes fulfill this role, such as upland lakes in Wales and rivers, appear to support the most stable and persistent populations.

The following conclusions can be reached on the dynamics of floating water-plantain metapopulations:

- Populations are capable of persisting at single sites for hundreds of years.
- The species is capable of colonising sites that are either already suitable or become suitable.
- A large proportion of site records represent short-term or failed colonisation for only one year.
- It is likely that the floating water-plantain has a capacity for extended dormancy, probably as seed. This could be as long as 15 years, but this has not yet been confirmed.
- In most lowland sites, the floating water-plantain appears to occur as dynamic metapopulations, where the metapopulation will always support some populations, but individual populations may only survive for relatively short periods.
- It is likely that long-term stable populations function as inocula for colonisation of new and temporarily suitable sites. Many such colonisation attempts appear to be unsuccessful. However, they will play a vitally important role in the long-term survival of metapopulations.
- There is insufficient information to assess limiting factors adequately. Distribution and abundance appear from available evidence to be restricted primarily by dispersal capacity, habitat availability and succession. There is a need for research to address these factors.
- It is likely that genetic exchange in perennial vegetative populations occurs through the occasional establishment of annual flowering populations arising from dispersal of plantlets.
- *L. natans* has undergone a significant decline in some areas of some countries (particularly Germany and England) but populations elsewhere seem stable and may be increasing through colonisation of newly created wetlands.
- The main causes of local declines appear to be the natural loss of populations through succession without replacement due to a lack of suitable alternative sites. Acidification may also be a factor. There is no strong evidence to demonstrate that other factors are implicated, although the spread of some invasive alien plant species (such as *Crassula helmsii*) may constitute a threat.
- *L. natans* can be found in Belgium, Denmark, France, Germany, the Republic of Ireland, the Netherlands, Norway, Poland, Spain, Sweden and UK. It can be defined as extending from southern Norway and Sweden in the north, through the Republic of Ireland and France to northern Spain, and east to Poland.
- There is no justification for inclusion of the floating water-plantain on the Global Plant Red Data List. However its inclusion on local or regional Red Lists, particularly within Germany and the UK in relation to English populations, is eminently justified.
- The main stronghold for the floating water-plantain is France, although some areas such as southeastern Germany and Wales support important concentrations. A comprehensive survey of populations in France, Poland and Ireland is vital, to enable accurate assessment of the distribution of population strongholds. It is also imperative that known populations are subject to monitoring.
- There are, as yet, insufficient data to precisely specify the substrate type requirements of floating water-plantain. Accurate recording of substrate during monitoring and surveillance should allow a picture of substrate associations to be developed.
- Disagreement in the literature over the pH requirement or tolerance of floating water-plantain is such that no conclusions can be reached. It appears likely that natural pH levels are rarely, if ever, a constraint on populations. However, as concern has been expressed over potential loss of populations due to acidification, further research would be justified.

Further research and survey

This section presents a brief summary of work needed to improve our understanding of the ecology of *L. natans* in different parts of its global range. It also describes the information required for monitoring British populations.

Current global status of *L. natans*

Assess the need for conservation at an international, national and regional level.	Current distribution and extent of populations and metapopulations.	Detailed survey similar to recent surveys in Wales. Main focus on France, Ireland and Poland. Data compilation and surveillance in all others areas.

Current UK status

Informed targeting of conservation action.	Current distribution and extent of populations and metapopulations.	Detailed survey in western Scotland and non-canal sites in the West Midlands; compilation of all recent data from canal surveys.

Annual flowering population dynamics

Lowland metapopulation management.	Size of populations making up metapopulations; factors influencing metapopulation dynamism; means of dispersal.	Systematic monitoring of the size and % cover of populations within each metapopulation; collection of phytosociological quadrat data. Delimitation of all metapopulations.

Perennial flowering population dynamics

Lowland metapopulation management.	Size of populations making up metapopulations; factors suppressing succession; means of dispersal.	Systematic monitoring of the size and % cover of populations within each metapopulation; collection of phytosociological quadrat data. Delimitation of all metapopulations.

Perennial vegetative population dynamics

Lowland metapopulation management.	Size of populations making up metapopulations; factors suppressing succession; means of dispersal.	Systematic monitoring of the size and % cover of populations within each metapopulation; collection of phytosociological quadrat data. Delimitation of all metapopulations.

Limiting factors

Factors suppressing succession

Metapopulation management.	Natural processes operating within waterbodies that suppress succession.	Collection of quadrat data; review of management history and natural dynamics of waterbodies.

Invasive aliens

Site or waterbody conservation.	Field data measuring the degree to which invasive aliens displace *L. natans* populations.	*In-situ* monitoring.

Chemical tolerance

Site or waterbody conservation.	Tolerance to acidity, and increases in nutrient levels.	*Ex-situ* experimental management; *in-situ* monitoring of water and substrate chemistry collected regularly or in winter.

References

Arber A (1920). *Water Plants*. Cambridge University Press, Cambridge.

Arts GHP and den Hartog C (1990). Phytogeographical aspects of the West European soft-water macrophyte flora. *Acta Botanica Neerlandica* 39, 369–378.

Arts GHP, van der Velde G, Roeloffs JGM and van Swaay CAM (1990a). Successional changes in the soft-water macrophyte vegetation of (sub) Atlantic, sandy, lowland regions during this century. *Freshwater Biology* 24, 287–294.

Arts GHP, Roelofs JGM and De Lyon MJH (1990b). Differential tolerances among soft-water macrophyte species to acidification. *Canadian Journal of Botany* 68, 2, 127–2134.

Balocco-Castella C (1988). *Les macrophytes aquatiques des milieux abandonées par le Haut-Rhône et l'Ain: diagnostic phyto-écologique sur l'évolution et le fonctionnement de ces écosystèmes*. Unpublished PhD Thesis, University C. Bernard, Lyon, France.

Bornette G and Amoros C (1991). Aquatic vegetation and hydrology of a braided river floodplain. *Journal of Vegetation Science* 2, 497–512.

Bornette G, Amoros C, Cestella C & Beffy J (1994). Succession and fluctuation in the aquatic vegetation of two former Rhone River channels. *Vegetatio* 110, 171–184.

Bornette G and Heiler G (1994). Environmental and biological responses of former channels to river incision: a diachronic study on the Upper Rhône River. *Regulated Rivers Research and Management* 9, 79–92.

Bournérias M (1979). *Guide des Groupements Végétaux de la Région Parisienne* (2nd ed). Société d'Edition d'Enseignement Supérieur, Paris.

Brewis PB, Bowman P & Rose F (1996). *The Flora of Hampshire*. Harley Books, Colchester.

Briggs JD (ed.) (1988). *Montgomery Canal Ecological Survey, Survey Report 1985–1988*. British Waterways, Gloucester.

Brown AE, Burn AJ, Hopkins JJ & Way SF (1997). *The Habitats Directive: Selection of Special Areas of Conservation in the UK*. JNCC Report No. 270. Joint Nature Conservation Committee, Peterborough.

Broyer J, Curtet L, Maillier S & Bove JJ (1997). Incidences de la gestion des étangs piscicoles de la Dombes sur la flore aquatique remarquable. *Ecologie*, 28, 323–336.

Buchmann SL & Nabhan GP (1996). *The forgotten pollinators*. Island Book, Washington, D.C.

Casper SJ & Krausch H-D (1980). *Sußwasserflora von Mitteleuropa. 23, Pteridophyta und Anthophyta 1. Lycopodiaceae bis Orchidaceae*. Gustav Fischer, Stuttgart.

Caussin O (1907). *Flore descriptive du littoral*. Picard, Paris.

Charlton WA (1973). Studies in Alismataceae II. Inflorescences of Alismataceae. *Canadian Journal of Botany* 51, 775–789.

Clapham AR, Tutin TG & Warburg EF (eds) (1962). *Flora of the British Isles* (2nd ed). Cambridge University Press, Cambridge.

Cook CDK (1983). Aquatic plants endemic to Europe and the Mediterranean. *Botanische Jahrbücher für Systematik* 103, 539–582.

Cook CDK, Gut BJ, Rix EM, Schneller J & Seitz M (eds) (1974). *Water Plants of the World*. Junk, The Hague.

Corillion R (1981). *Flore et Végétation de la Vallée de la Loire (Cours occidental : de l'Orléanais à l'estuaire)*. Jouve, Paris.

Czeczott H (1926). The Atlantic element in the flora of Poland. *Bulletin de l'Academie Polonaise des Sciences et des Lettres Cl. des Sc. Mathem et Naturelle Series B. Cracovie* 361–407.

Danton P & Baffray M (1995), *Inventaire des plantes protégées en France*. Éditions Nathan, Paris.

Devillers P, Devillers, Terschuren J and Ledant JP (1991). Habitats of the European Community (CORINE Biotopes Manual). Office for Official Publications of the European Communities, Luxembourg.

D'Hose R & de Langhe JE (1977). Nieuwegroeiplaatsen van zeldzame planten in Belgie V. *Bull. Soc. Roy. Bot. Belgique* 112, 21–34

Dierssen K (1981). Littorelletea communities and problems of their conservation in Western Germany. *Colloques phytosociologiques* 10, 324–331.

Driscoll RJ (1985). Floating water-plantain *Luronium natans* in Norfolk. *Transactions of the Norfolk and Norwich Naturalists' Society*, 27, 43–44.

ECE (Economic Commission for Europe) (1991) *European Red List of globally threatened animals and plants*. United Nations, New York .

English Nature (in prep.) *Species Action Plan* – Luronium natans. English Nature, Peterborough.

Ferguson C (1991). *The distribution of the floating water-plantain (*L. natans *L. Raf.) in Great Britain and Ireland*. Unpublished BSc (Hons) degree dissertation, Loughborough University

Fournier P (1961). *Les Quatre Flores de la France Corse Comprise*. Paul Lechevalier, Paris.

Fritz O (1989). Flytsvalting, *L. natans*, funnen i Halland (1988). (A find of *L. natans* in the province of Halland, SW Sweden). *Svensk Bot. Tidskr.* 83, 2, 135–136.

Garve E (1994). Atlas der gefährdeten Farn- und Blütenpflanzen in Niedersachsen und Bremen Kartierung 1982–1992. *Naturschutz Landschaftspla. Niedersachs* 30, 1–895.

Gaudillat V (in prep). The floating water-plantain (L.) Raf. In: *Connaissance et gestion des habitats et des espèces d'intérêt communautaire. Tome 2 – Espèces, Vol 1. Flore*. Muséum National d'Histoire Naturelle, éd La Documentation Française.

Greulich S Barrat-Segretain, M-H & Bornette G (2001). Basal rosette or floating leaf canopy – an example of plasticity in a rare aquatic macrophyte. Accepted for *Hydrobiologia*.

Greulich S, Bornette G , Amoros C & Roelefs JGM (2000a). Investigation on the fundamental niche of a rare species, an experiment on establishment of the floating water-plantain. *Aquatic Botany* 66, 209–224.

Greulich S, Bornette G & Amoros C (2000b). Persistence of a rare aquatic species along gradients of disturbance and sediment richness. *Journal of Vegetation Science* 11, 415–424.

Haeupler H & Schönfelder P (1989). *Atlas der Farn- und Blütenpflanzen der Bundesrepublik Deutschland*. Eugen Ulmer, Stuttgart.

Hanspach D (1991). Zur Verbreitung und Ökologie von *Eleogiton fluitans* (L) Link in der DDR. *Gleditschia* 19, 101–110.

Hanspach D & Krausch HD (1987). Zur Verbreitung und Ökologie von *L. natans* (L.) Raf. in der DDR. *Limnologica* (Berlin) 18, 167–175.

Hardtke H-J & Ihl A (2000). *Atlas der Farn- und Samenpflanzen Sachsens. Materialien zu Naturschutz und Landschaftspflege (2000)*. Sächsiches Landesamt fuer Umwelt und Geologie, Dresden.

Haslam S, Sinker C & Wolseley (1975). British Water Plants. *Field Studies* 4, 243–351.

Haury J (1985). Etude Ecologique des Macrophytes du Scorff (Bretagne-Sud). These Doct.-Ing. Ecologie, Université Rennes I, Rennes, France.

Haury J (1988). Macrophytes du Trieux (Bretagne-Nord). Les ensembles floristiques. *Bull. Soc. Sc. Nat. Ouest de la France*, Nouvelle Série 10, 135–150.

Haury J (1996). Les macrophytes. *Un outil de diagnostic de la qualité du cours principal de l'Elorn.* INRA Lab. Ecol. Hydrobiol. and ENSA DEERN Syndicat Mixte d'Aménagement de l'Elorn et du Daoulas. Ecol. Sci. Phytosan, Rennes.

Haury J & Muller S (1991). Variations écologiques et chorologiques de la végétation macrophytique des rivières acides du Massif Armoricain et des Vosges du Nord (France). *Revue des Sciences de l'Eau* 4, 463–482.

Haury J, Thiebaut G & Muller S (1994). Les associations rhéophiles des rivières acides du Masssif Armoracain, de Lozère et des Vosges du Nord, dans un contexte Ouest-Européen. *Colloques Phytosociologiques* 23, 145–168.

Hegi G (1981). *Illustrierte Flora von Mitteleuropa. Bd I, 3.* Auflage, Berlin, Hamburg.

Henry CP, Amoros C & Bornette G (1996). Species traits and recolonization processes after flood disturbances in riverine macrophytes. *Vegetatio* 122, 13–27.

Holmboe J (1930). Spredte bidrag til Norges Flora. I. *Nyt magazin for naturvidenskaberne* 68, 1, 19–151.

Hultén E (1950). *Atlas of the Distribution of Vascular Plants in NW Europe*. Stockholm.

Hultén E (1971). *Atlas över växternas utbredning i Norden* (2nd ed), P Kartografiska Institutet, Stockholm.

IUCN (2001). IUCN Red List Categories, Version 3. 1. Prepared by the IUCN Species Survival Commission IUCN, Gland, Switzerland, and Cambridge, UK.

Jones RA & Rich TCG (1998). *Luronium natans/Baldellia ranunculoides/Alisma*. In: Rich TCG & Jermy AC (eds). *Plant crib*. Botanical Society of the British Isles, London.

Kaplan K (1992). Farn- und Blütenpflanzen nährstoffarmer Feuchbiotope. *Metelener Schriftenreihe für Naturschutz* 3, 1–116.

Kaplan K (1993). Heideweihergefährdung durch Immissionen. LÖLF - Mitteilungen 1, 93, 10–17.

Kaplan K & Jagel A (1997). *Atlas zur Flora der Kreise Borken, Coesfeld und Steinfurth - eine Zwischenbilanz Meteler Schriftenreihe für Naturschutz* 7. Biologisches Institut. Metelen e.V. , Metelen.

Kaplan K & Lenski H (1989). Zur Pflanzenbesiedlung feuchter nährstoffarmer Pionierstandorte in der Westfälischen Bucht. *Natur u. Heimat* 49, 49–56.

Kay QON & John RF (1995). *The conservation of scarce and declining plant species in lowland Wales. Population genetics, demographic ecology and recommendations for future conservation in 32 species of lowland grassland and related habitats*. Science Report No. 110, Countryside Council for Wales, Bangor.

Kay QON, John RF & Jones RA (1999). Biology, genetic variation and conservation of *Luronium natans* (L) Raf. in Britain and Ireland. *Watsonia* 22, 4, 301–315.

Køie M (1944). Fordelingen af vegetationen i Skern aa og Tilløb (The distribution of the vegetation in the River Skern and its tributaries). *Botanisk Tidsskrift* 46, 239–250.

de Langhe JE, Delvosalle L, Duvigneaud J, Lambion J & Vanden Berghen C (1978). *Nouvelle Flore de la Belgique, Du Grand Duché de Luxembourg, du Nord de la France et des Regions Voisines*. Deuxième édition. Jardin Botanique National de Belgique, Meise.

Lansdown RV & Evans SB (2001). Three-lobed crowfoot *Ranunculus tripartitus* DC in Wales. *BSBI Welsh Bulletin* 68, 21–22.

Lansdown R V & Stewart NF (1999). *The conservation status of tassel stonewort (*Tolypella intricata*) in Britain.* Interim Report No. 1. Plantlife Report No. 122. Plantlife, London.

Lansdown RV (2000). *A preliminary report on the ecology and distribution of threatened British wetland plants in southern continental Europe. Plantlife Report No. 144. Plantlife, London.*

Libbert W (1940). Pflanzensoziologische Beobachtungen während einer Reise durch Schleswig-Holstein im Juli (1939). *Beiträge zur Systematik und Pflanzengeographie* 121, 92–130.

Lid J (1952). *Norsk Flora*. Det Norske Samlaget, Oslo.

Lockton A & Whild S (1995). *Rare plants of Shropshire*. Shrewsbury Museums Service, Shrewsbury.

Maessen M, Roeloffs JGM, Bellemakers MJS & Verheggen GM (1992). The effects of aluminium, aluminium/calcium ratios and pH on aquatic plants from poorly buffered environments. *Aquatic Botany* 43, 115–127.

Mennema J, Quené-Boterenbrood AJ & Plate CL (1985). *Atlas van de Nederlandse Flora. 2. Zeldzame en vrij zeldzame planten Bohn*. Scheltema and Holkema, Utrecht.

Meriaux J-L (1981). La classe des Potametea dans le nord-ouest de la France. *Colloques phytosociologiques* 10, 115–129.

Meriaux J-L (1982). Espèces rares ou menacées des biotopes lacustres et fluviatiles du nord de la France. *Natura Mosana* 34, 177–194.

Meriaux J-L & Wattez J-R (1981). Groupements vegetaux aquatiques et subaquatiques de la valée de la Somme. *Colloques phytosociologiques* 10, 369–413.

Merkel J (1982). *L. natans* (L.) Raf. ein Neufund in Bayern. *Gottinger Flor. Rundbr*. 16, 1–2, 43–48.

Mikkelsen VM (1943). Udbredelsen af Juncaginaceae, Alismataceae og Hydrocharitaceae i Denmark (The distribution of the Juncaginaceae, Alismataceae and Hydrocharitaceae in Denmark). *Botanisk Tidsskrift* 47, 65–94.

Moss B (1995). *Ecology of Fresh Waters. Man and Medium*. Blackwell Science, Oxford.

van den Munckhof PJJ (2000). Glauconietrijke afzettingen in the Peel region. Een ijzersterke basis voor behoud en ontwikkeling van voedselarme, natte milieus! (Glauconite-rich deposits in the Peel region. An iron basis for conservation and development of nutrient poor, wet environments). *Natuurhistorisch Maandblad* 89, maart, P, 43–52.

Netien G (1993). *Flore Lyonnaise*. Edition de la Société Linnéenne de Lyon, Lyon.

Oberdorfer E (1970). Pflanzensoziologische Exkursionsflora für Süddeutschland und die angrenzenden Gebiete. 3. Auflage, Stuttgart.

van Ooststroom SJ & Reichgelt TJ (1964). Alismataceae. *Flora Neerlandica* 1, 1–15.

Perdigó MT (1983). L'estanyó, un petit estany interessant a la Vall d'Aràn. *Collectanea Botanica (Barcelona)* 14, 511–514.

Pignattti S (1982). *Flora d'Italia* 3, 319.

Plate CL (1985). *L. natans*. In: Mennema J, Quené-Boterenbrood AJ &Plate CL (1985). *Atlas van de Nederlandse flora, deel 2 (Atlas of the Dutch flora)*. Bohn, Scheltema and Holkema, Utrecht.

Poinsot H (1972). *Flore de la Bourgogne*. Librairie de l'Université, Dijon.

Preston CD & Croft JM (1997). *Aquatic Plants in Britain and Ireland*. Harley Books, Colchester.

Preston CD & Hill MO (1997). The geographical relationships of British and Irish vascular plants. *Botanical Journal of the Linnean Society* 124, 1, 1–120.

Provost M (1993). *Atlas de répartition des plantes vasculaires de Basse-Normandie*. Université de Caen, Caen.

Ridley HN (1930). *The dispersal of plants throughout the world*. L Reeve & Co, Ashford.

Robbe G (1984). Inventaire dynamique des espèces rares du Morvan (1re partie). *Bull. Trim. Soc. Hist. Nat. Autun*. 110, 3–36

Rodriguez-Oubiña J and Ortiz S (1991). *L natans* (Alismataceae) in the Iberian Peninsula. *Willdenowia* 21, 77–80,

Rodwell JS (1995). *British plant communities. Vol. 4. Aquatic communities, swamps and tall-herb fens*. Cambridge University Press, Cambridge.

Roelofs JGM (1983). Impact of acidification and eutrophication on macrophyte communities in soft waters in the Netherlands. I. Field Investigations. *Aquatic Botany* 17, 139–155.

Roelofs JGM, Bobbink R, Brouwer E & de Graaf MCC (1996). Restoration ecology of aquatic and terrestrial vegetation on noncalcareous soils in the Netherlands. *Acta Botanica Neerlandica* 45, 517–541.

Roelofs JGM, Schuurkes JAAR & Smits AJM (1984). Impact of acidification and eutrophication on macrophyte communities in soft water. II. Experimental studies. *Aquatic Botany* 18, 389-411.

Saint-Lager Dr (1883). *Catalogue des plantes vasculaires de la flore du bassin du Rhône*. Librairie H. Georg, Lyon.

Schaminée JHJ, Weeda EJ & Westhoff V (1995). *Plantengemeenschappen van wateren, moerassen en natte heiden; de vegetatie van Nederland, deel 2 (Plant communities of waters, marshes and wet heath; the vegetation of the Nettherlands, part 2)*. Opulus Press, Uppsala-Leiden.

Schaminée JHJ, Westhoff V & Arts GHP (1992). Die Strandlingsgesellschaften (Littorelletea Br -BL et Tx 43) der Niederlande, in europäischen Rahmen gefabt. *Phytocoenologia* 20, 529–558.

Sell P & Murrell G (1996). *Flora of Great Britain and Ireland. 5. Butomaceae-Orchidaceae*. Cambridge University Press, Cambridge.

Smits AJM, Kleufers RMJC, Kok CJ & Van Der Velde G (1990a). Alcohol dehydrogenase isoenzymes in the roots of some nymphaeid and isoetid macrophytes. Adaptations to hypoxic sediment conditions. *Aquatic Botany* 38, 19–27.

Smits AJM, Laan P, Thier RH & Van Der Velde G (1990b). Root aerenchyma, oxygen leakage patterns and alcoholic fermentation ability of the roots of some nymphaeid and isoetid macrophytes in relation to the sediment type of their habitat. *Aquatic Botany* 38, 3–17.

Stewart A, Pearman DA & Preston CD (1994). *Scarce plants in Britain*. Joint Nature Conservation Committee, Peterborough.

Szmeja J & Clement B (1990). Comparison of the structure and determinism of *Littorella uniflora* in Pomerania (Poland) and Brittany (France). *Phytocoenologia* 19, 123–148.

Tutin TG, Heywood VH, Burges NA, Moore DM, Valentine DH, Walters SM & Webb DA (eds) (1980). *Flora Europaea. 5. Alismataceae to Orchidaceae*. Cambridge University Press, Cambridge.

Wade PM & Darwell A (2000). *Survey of key sites within West Midlands Meres and Mosses Natural Area for the Floating Water-plantain*. Unpublished report to English Nature. English Nature, Peterborough.

Walter KS & Gillet HJ (eds)(1998). *1997 Red List of Threatened Plants*. Compiled by the World Conservation Monitoring Centre. IUCN – The World Conservation Union, Gland, Switzerland and Cambridge, UK.

Weeda EJ, Westra R, Westra C & Westra T (1991). *Nederlandse oecologische flora, deel 4 IVN (Dutch Ecological Flora)*. VARA en Vewin, Amsterdam.

Willby NJ & Eaton JW (1993). The distribution, ecology and conservation of *L. natans* (L) Raf. in Britain. *Journal of Aquatic Plant Management* 31, 70–76.

de Wit HCD (1964). *Aquarium Plants*. Blandford, London.

Wittig R (1982). The effectiveness of the protection of endangered oligotrophic-water vascular plants in nature conservation areas of North Rhine-Westphalia (Federal Republic of Germany). Studies on Aquatic Vascular Plants, Proc. In: Symoens JJ, Hooper SS & Compere P (eds.). *Colloquium on Aquatic Vascular Plants*. Royal Botanical Society of Belgium, Brussels, 418–424.

Wittig R (1995). Naissance et disparition de l'Eleocharitetum multicaulis, une végétation caractéristique des étangs temporaires de bruyéres au nord-ouest de l'Europe Centrale. *Colloques Phytosociologiques* 24, 131–140.

Wittig R (1996). Schutz der vegetation temporärer Heideweiher durch Biotop - Neuschaffung . *Naturschutz und landschaftsplanung* 28, 112–117.

Wittig R & Pott R (1982). Die Verbreitung von Littorelletea-Arten in der Westfalischen. *Bucht Decheniana (Bonn)* 135, 14–21.

Zarzycki K, Wojewoda W & Heinrich W (eds.) (1992). List of Threatened Plants in Poland, 2nd ed. Polish Academy of Sciences, W. Szafer Institute of Botany, Cracow, 98 pp.

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