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ECOLOGY

The Distribution, Ecology and Conservation of *Luronium natans* (L.) Raf. in Britain

NIGEL J. WILLBY AND J. W. EATON[1]

ABSTRACT

Despite a wide ecological amplitude, *Luronium natans* remains a rare aquatic plant endemic to Europe. The main populations occur in Britain, where *Luronium* is found in clear water lakes, navigation canals and ponds with widely ranging water chemistry and associated plant communities. The spread of the plant this century from upland to lowland sites via an interconnecting system of waterways is chronicled. *Luronium* is a permanent member of the flora in lakes where various combinations of oligotrophy and disturbance by waves produce a stable low biomass, open-structured vegetation. It also occurs prolifically in more productive waters as an early colonist of recently disturbed, often artificial habitats, but in later stages of succession is out-competed by more vigorous species. *Luronium* is, therefore, transient or erratic in these artificial habitats, because it depends on sustained human disturbance to arrest hydroseral succession and maintain its niche. Dealing primarily with canal sites, the problems of habitat management and conservation of *Luronium* are discussed.

Key words: oligotrophic, canal, disturbance, management.

INTRODUCTION

Luronium natans (L.) Raf., (Alismataceae) the Floating Water-plantain, is a rare aquatic plant, endemic to Europe, whose distribution is decreasing in most areas. In Great Britain its natural habitat is mostly oligotrophic, upland lakes, but since the late nineteenth century it has shown a notable spread down into the apparently quite different habitat of eutrophic, lowland navigable canals, where its main populations are now located. This change raises interesting questions for the aquatic botanist. What features have permitted this extension of the plant's distribution? How can they be sustained to conserve the species in its new artificial habitat? This paper offers a preliminary attempt to answer these questions.

Luronium natans is a small, perennial, stoloniferous aquatic plant with a heterophyllous growth form. The floating-leaved form (f. *repens* Buch.), found in shallow water or occasionally along channel margins (Hanspach and Krausch 1987) and on exposed wet mud (pers. obs.), has small, ovate leaves carried on ascending petioles arising either from a submerged basal rosette or, in emergent plants, directly from the stolon. The three-petalled flowers, borne usually at the water surface, are small (12 to 16 mm across), white, hermaphrodite and normally solitary. The fruits (achenes) comprise small, buoyant, single-seeded capsules which are beaked and finely ribbed and are probably dispersed by both drift and waterfowl.

The submerged form (f. *submersum* Glück) consists of shallow-rooting rosettes of narrow tapering leaves. It is wholly vegetative and generally occurs in faster flowing water or where light intensities are reduced by shading, turbidity, dystrophy or as depth increases (up to 2 m). Vegetative propagules in the form of buoyant, viable plants are yielded by fragmentation of the stolons and are dispersed by drift.

Luronium has a distribution centered on Belgium, France, Great Britain, the Netherlands and northern Germany (Hanspach and Krausch 1987). Outlying populations have been reported from Scandinavia (southern Sweden, Fritz 1989; west Denmark and south Norway, Björkqvist 1961). Tutin *et al.* (1980) mention occurrences in Spain, Italy and Yugoslavia, extending eastwards into Bulgaria, Poland, and the regions of southwest and possibly Baltic Russia. They consider it to be extinct in Czechoslovakia and Romania. Its recorded habitats include lakes, reservoirs, ponds, bog pools, ditches, canals and slowly flowing rivers.

Throughout its continental range, *Luronium* is reportedly extremely scarce (Hanspach and Krausch 1987) and many remaining sites are now endangered (Wittig and Pott 1982, Fritz 1989, Meriaux 1982). Serious declines of *Luronium* or its phytosociological grouping have been documented in the Netherlands (*e.g.* Arts *et al.* 1990) and Germany (Wittig and Pott 1982, Hanspach and Krausch 1987) as a result of

[1]Research student and Lecturer, respectively. Department of Environmental and Evolutionary Biology, School of Life Sciences, University of Liverpool, P. O. Box 147, Liverpool L69 3BX, England.

acidification or eutrophication of formerly oligotrophic waters (Wittig 1982, Roelofs 1983, Arts *et al.* 1990). This has led to its inclusion in the IUCN list of Rare, Threatened and Endemic Plants as a species vulnerable to extinction (Lucas and Walters 1976). Recently *Luronium* was also added to Annexe I of the Berne Convention on the Conservation of European Wildlife and Natural Habitats, which affords special protection for listed plants and their habitats.

In Britain *Luronium* is scarce, but not sufficiently rare to justify inclusion in the Red Data Book for Vascular Plants (Perring and Farrell 1983), and it seems probable that Britain supports the bulk of the remaining world population. However, to honor its obligation to the Berne Convention, the British government has added *Luronium natans* to Schedule 8 of the Wildlife and Countryside Act 1981, making picking, uprooting or willful destruction of the plant illegal.

To date, an ecological appraisal of the plant and comprehensive statement of its current status in Britain are lacking. As these are prerequisites for informed conservation action, this paper aims to offer information on both these aspects.

METHODS

Changes in the distribution of *Luronium* in Great Britain were analyzed from the British Biological Records Centre data, complemented by Country Floras and other records from reports of botanical excursions, the general ecological literature, details of herbarium specimens, unpublished data from canal surveys and personal observations made during extensive surveys of canal vegetation since 1989. These sources were also used to define the plant communities associated with *Luronium* in its two principal habitats, *viz.* lakes and canals. For sites where *Luronium* no longer occurs, County Floras were used to reconstruct the flora at or around the time it was present. Seddon's (1972) extensive work on Welsh lakes in the early 1960s provided additional information on communities containing *Luronium* and on associated water chemistry. Analyses of Cumbrian lake waters since 1953 (Carrick and Sutcliffe 1982) and of canal waters (regional water authorities and original data) were also used.

RESULTS

Ecology in Main Habitats

i. Lakes

Luronium has a long recorded history in some lakes, particularly those in the uplands of North and Mid-Wales. It occurred at Llanberis in Snowdonia from at least as early as 1729 and there are nineteenth century records from 12 other lakes in this region. Since 1960 *Luronium* has been reported from at least 20 lakes in upland Wales. Until the end of the last century it was also known from several lakes in Cumbria.

Seddon (1972) studied 70 Welsh lakes varying in area from 0.001 to 1.53 km^2 and at altitudes from 4 to 701 m. *Luronium* was found in 11 of these water bodies (area 0.08 to 1.01 km^2; altitude 91 to 454 m), being notably almost confined to larger lakes in the high altitude part of its range, with smaller water bodies becoming colonized only in lower lying areas. This trend also applied to the former Cumbrian populations (lake area 0.64 to 8.94 km^2; altitude 44 to 145 m).

Seddon (1972) also provides analyses of water chemistry for six of the lakes in which *Luronium* was found. These data are summarized in Table 1. Combined with other descriptive evidence, they support the general view in the botanical literature that *Luronium* is a plant of soft, slightly acid waters with low nutrient concentrations.

TABLE 1. COMPARISON OF SELECTED WATER CHEMISTRY PARAMETERS BETWEEN WELSH LAKES[1] AND THREE CANAL SITES[2].

Parameter	Welsh lakes	Canals		
		Mont.	Roch.	Ash.
Conductivity (μmhos)	53 (33-70)	147 (66-270)	383 (318-485)	210 (145-200)
pH	6.5 (5.5-7.6)	7.3 (6.7-8.8)	7.3 (6.9-9.2)	7.5 (6.7-8.3)
Ca^{2+} (mg l^{-1})	2.7 (1.3-4.5)	22.5 (10.7-58.8)	17.7 (12.7-24.6)	38.5 (12-65)

[1]Mean of 6 sites, from Seddon (1972); Ca^{2+} estimated from total hardness values.

[2]Mont. = Montgomery; (3 to 10 replicate samples from 19 sites) from Briggs (1988); Roch. = Rochdale; (spot samples from 38 sites) from Shimwell (1984); Ash. = Ashton Canal plus Huddersfield Narrow Canal to Stalybridge and Peak Forest Canal to Hyde (3 to 7 replicate samples from 10 sites). Upper number is the mean, bracketed numbers are the range.

The vegetation in lakes in which *Luronium* is found (Table 2) normally includes *Lobelia dortmanna* L., *Littorella uniflora* (L.) Aschers., *Isoetes lacustris* L. and *Callitriche hamulata* Kutz. ex Koch, a core group characteristic of oligotrophic waters and often accompanied by *Juncus bulbosus* L., *Potamogeton polygonifolius* Pourr., *P. natans* L., *Myriophyllum alterniflorum* DC., *Nuphar lutea* (L.) Sm. and *Sparganium angustifolium* Michx. The emergent vegetation at these sites is also typical of upland, nutrient-poor waters and includes *Equisetum fluviatile* L., *Carex rostrata* Stokes and *Menyanthes trifoliata* L. Although this analysis is confined to recent or current sites in Wales, historical evidence

TABLE 2. INCIDENCE OF PRINCIPAL MACROPHYTES IN LAKES (14 sites) OR IN CANAL SECTIONS CONTAINING *Luronium*[1].

Lake species	Frequency	Canal Species	Frequency		
			Mont.[a]	Roch.[b]	Ash.[c]
*Callitriche hamulata**	3	*Acorus calamus*	2		
Carex rostrata	2	*Alisma plantago-aquatica*	2	1	1
Elatine hexandra	1	*Butomus umbellatus*	1		
Eleocharis palustris	1	*Callitriche hamulata**	3		1
Equisetum fluviatile	3	*C. hermaphroditica*	1	1	
*Glyceria fluitans**	1	*C. stagnalis*	2	1	
Hydrocotyle vulgaris	1	*Ceratophyllum demersum*	3		
Isoetes lacustris	3	*Elodea canadensis*	3	3	
I. setacea	1	*E. nuttallii*	3	2	4
Juncus bulbosus	2	*Glyceria fluitans**		1	
Littorella uniflora	3	*G. maxima*	4	4	4
Lobelia dortmanna	3	*Hottonia palustris*		1	
Menyanthes trifoliata	2	*Hydrocharis morsus-ranae*	[1]		
*Myriophyllum alterniflorum**	2	*Lemna minor*	4	4	4
*Nuphar lutea**	2	*L. trisulca*	2		2
Nymphaea alba	1	*Myosotis scorpioides*	2		1
*Potamogeton berchtoldii**	1	*Myriophyllum alterniflorum**	1		
*P. natans**	2	*M. spicatum*	2		
P. polygonifolius	2	*Nitella sp.*	3		
Eleogiton fluitans	1	*Nuphar lutea**	2		
Sparganium angustifolium	2	*Polygonum amphibium*	1		
Subularia aquatica	1	*Potamogeton alpinus*	[2]		1
		*P. berchtoldii**	2	2	1
		P. compressus	3		3
		P. crispus	2	1	1
		P. epihydrus		2	
		*P. natans**	4		4
		P. obtusifolius	4		
		P. pectinatus	[2]		1
		P. perfoliatus	[2]		1
		P. praelongus	[1]		
		P. trichoides			1
		Ranunculus circinatus	1		
		Sagittaria sagittifolia			4
		Sparganium emersum	4	3	3
		S. erectum	4		
		Typha latifolia	1		

[1](a = maxima during 1985 to 1987, based on 21 to 31 sections of 1 km; b = 39 bridge lengths (mean length 550 m) surveyed 1983 to 1984; c = 10 bridge lengths (mean length 500 m) surveyed 1990 to 1992.) 1 = 20-39% of sites; 2 = 40-59%; 3 = 60-79%; 4 = >80%. Bracketed values are historical records for species formerly of more widespread distribution. * = principal species common to both habitats. Site details and sources as for Table 1.

indicates that the former Cumbrian populations had similar associations of species.

ii. Canals

Luronium first appeared on the canal system near Llangollen, N. Wales, about 1860. The Llangollen Canal receives water from the River Dee, which drains a number of upland catchments containing *Luronium*. There followed a period of rapid expansion along the canals of Cheshire, Shropshire and the Welsh Border counties coinciding with a decline in the use of these canals by freight boats, as competition with the railways intensified (Murphy *et al.* 1982). *Luronium* then continued to spread until by the late 1930s it had colonized much of the Macclesfield Canal and part of the Manchester canal system (including water thermally polluted by mill effluents, Shaw 1963). It subsequently became established at various locations on canals in Staffordshire, the Midlands and Leicestershire and extended northward from Manchester along the Rochdale Canal into West Yorkshire, while consolidating existing populations. This pattern of colonization is consistent with the suggestion by Lousley (1970) that

Luronium spread eastward into lowland Britain from an original focus of distribution in the Welsh mountains via the interconnecting canal system (Figure 1). Today it remains well represented in the floras of several canals, although its overall range has contracted since 1960, following a rapid increase in propeller-driven recreational boat traffic on some of the waterways.

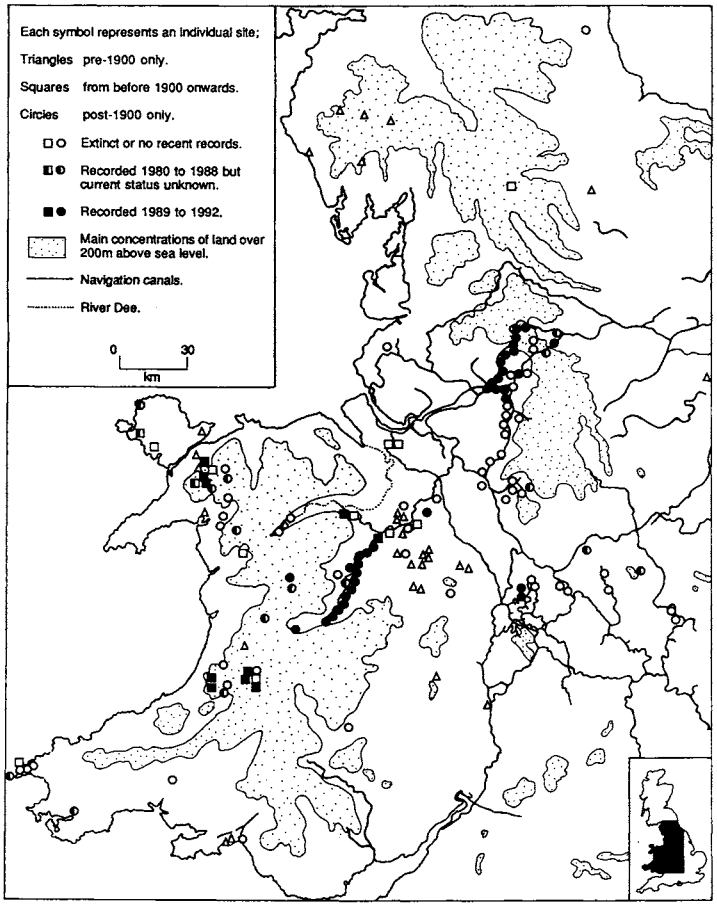


Figure 1. Diagrammatic representation of changes in the distribution of native *Luronium natans* populations in England and Wales since 1800 in relation to relief and the navigation canal system.

Compared to upland lakes (Table 1), canals have harder, more alkaline and calcium-rich waters with much higher major ion concentrations. Some populations occur at conductivities up to 800 µmho, far exceeding the range in Table 1, but are not listed there as information on the other environmental factors is not yet available.

Table 2 lists some of the principal species with which *Luronium* often coexists in canals, based on the three largest existing canal populations. This illustrates the diverse composition of the associated lowland floras and their complete contrast in character to upland lake communities, as is evident from the small number of species common to both lists.

Fringes of *Glyceria maxima* (Hartm.) Holmberg and a partial surface covering of *Lemna minor* L. are ubiquitous and *Elodea nuttallii* (Planch.) St. John and *Sparganium emersum* Rehm. are widespread. The canal communities are phytosociologically characteristic of the Potametea classes, with *Potamogeton compressus* L., *P. obtusifolius* Mert. and Koch, *P. crispus* L., *P. natans* and *P. berchtoldii* Fieb. the species most frequently encountered. In the Rochdale Canal, where *P. natans* and *P. compressus* are very scarce or absent, the morphologically similar *P. epihydrus* Raf., an alien species which naturalized from cotton mill waste in the early 1950s (Shaw 1963), may occupy an equivalent niche.

iii. Other Habitats

Luronium has been recorded from a variety of other freshwater habitats in Britain, including slow flowing rivers and streams, ditches, ponds, small lowland lakes or reservoirs and open water pools associated with fens or lowland raised bogs, for example on the Shropshire-Cheshire Plain. These records are concentrated in Wales or bordering counties and involve outlying sites, remote from the main center of distribition or originate from the mid-1800s, prior to the expansion of *Luronium* into lowland districts via the canal system.

Existing sites in this class are often situated on sandy peat and have clear, shallow, neutral or mildly acid water of variable base status. Many are poorly documented but it is known from historic records that most supported a flora characteristic of mesotrophic conditions at the time *Luronium* was present. The most distinctive and commonly associated species are *Echinodorus ranunculoides* (L.) Parl., *Eleogiton fluitans* (L.) Link, and *Apium inundatum* (L.) Reichb.f., with *Pilularia globularia* L., *Hypericum elodes* L., *Veronica scutellata* L., *Potamogeton gramineus* L. and *Sparganium minimum* Wallr. often also present. These species are occasionally found intermixed with others more characteristic of base-rich environments, such as *Potamogeton lucens* L. and *Hippurus vulgaris* L. The persistence of the isoetids *L. dormanna* and *Littorella* was, by contrast, a temporary feature of sites in the Shropshire meres. Running water sites are additionally characterised by the presence of *P. natans*, *N. lutea* and *M. alterniflorum*, while *M. trifoliata*, *E. fluviatile* and *C. rostrata* are of general occurrence.

In terms of their physical, chemical and vegetational characteristics, these sites are more typical of contemporary continental *Luronium* habitats, as described, for example, by Wittig and Pott (1982), Arts *et al.* (1990), than the two previous groups. Heavy losses during this century, due in part to drainage, agricultural improvements, nutrient enrichment and successional infilling are also reminiscent of the fate of

Luronium in continental Europe, although acidification, a widely noted factor in the decline of Littorellion communities on the continent, is not implicated in the loss of *Luronium* from equivalent habitats in Britain.

DISCUSSION

The ability to persist in plant communities, water types and local climates of very contrasting character proves *Luronium* to be a remarkably catholic species. Despite being traditionally regarded as a plant of soft, acid waters (Libbert 1940), it is clear that *Luronium* can thrive in the circumneutral to mildly alkaline, relatively base-rich waters found in canals and some other lowland habitats. Perhaps the only real significance of water chemistry to a plant of such wide ecological amplitude is as an influence on the composition and productivity of the vegetation with which it must coexist.

Initially, therefore, such a localized distribution seems anomalous. The one factor which unifies these diverse habitats, however, appears to be a permanent or temporary low abundance of competitively dominant macrophytes such as tall growing, but easily damaged, elodeids and marginal reedswamp species.

Upland oligotrophic lakes offer a chronically unproductive, periodically wave-disturbed habitat, the intermittent severity of which is often revealed only by a strandline accumulation of uprooted isoetid plants which may appear after gales. Low nutrient and inorganic carbon availability also require efficient nutrient harvesting and conservation mechanisms and cannot support the heavy demands of high biomass-density, competitive species for growth and repair of plant tissue. Here *Luronium* forms part of a disturbance and/or stress-tolerant vegetation, dominated by short, compact, robust, slow growing, evergreen plants with high belowground:aboveground biomass ratios (Hutchinson 1975, Spence 1982).

Shallow, lightly trafficked canals, a niche rare in continental Europe, are species rich, productive habitats where the stresses imposed by competitive species are curbed by the moderate disturbance of the boat movements (Murphy and Eaton 1983). Slowly flowing, unnavigated rivers subject to occasional scouring floods represent a comparable niche more often occupied by continental populations (*e.g.* Weigleb 1983).

In disused canals undergoing restoration, or more rarely in ponds and ditches, *Luronium* occurs as a prolific opportunistic colonist in the wake of severe disturbance by dredging or other clearance operations. Hanspach and Krausch (1987) describe the widespread occurrence of *Luronium* in recently cleaned or newly constructed drainage ditches in southeast Germany.

Small, sheltered or isolated sites may support a lo biomass of aquatic vegetation due to a fluctuating water lev infertile or poorly structured sediment, nutrient-poor or lo pH water, shading by an overhanging tree canopy or simp due to chance dispersal effects allied to water area or remo ness from a pool of suitable propagules.

In lowland areas outside canals, a high natural turnov of *Luronium* populations should be anticipated due to t ephemeral nature of the post-disturbance, pioneer nic (unless this is renewable) and the susceptibility of sma isolated populations to extinction simply through stochast fluctuations.

The absence of *Luronium* from habitats occupied by mo aggressive species, or its presence only as a relic pione species, indicates a weak competitive ability. In growth-strateg terminology (Grime 1977), *Luronium* habitats lie on a grad ent of stress and disturbance. Selection appears to favor ruderal strategy, but tolerance of the stresses imposed b low-nutrient concentrations, low pH or partial shading fro trees or more competitive aquatic species confers a wid ecological amplitude. Heterophylly may provide an adde dimension to phenotypic plasticity and may partly account fo the broad adaptability of *Luronium.*

CONSERVATION AND MANAGEMENT

Between 1900 and 1970, *Luronium* expanded its distribu tion in Britain. Upland populations, some with a recorde history of over 200 years, were largely stable and despite thei vulnerability seem to be continuing to resist the insidious threat of acidification via acid deposition (*cf.* Wade 1983). Early losses from lowland ponds and ditches, often due to habitat destruction (*e.g.* Sinker *et al.* 1985), were offset by expansion along canals. Despite suggestions in the popular botanical literature of an ongoing expansion (*e.g.* Rose 1981, Blamey and Grey-Wilson 1989), this trend has more recently reversed due to the decline of *Luronium* on canals where recreational boat traffic has increased, often greatly, over the last 30 years (*e.g.* Macclesfield Canal; Newton 1990). Nevertheless *Luronium* retains a relatively healthy status in Britain compared to continental Europe, and surviving lowland canal populations are clearly of increasing international importance (Briggs 1988). Several canals and lakes where *Luronium* occurs are now notified as Sites of Special Scientific Interest (SSSIs) and therefore protected by statute under the Wildlife and Countryside Act 1981.

In Wales some lake populations have persisted for centuries without specific protection. Geographical isolation in a sparsely populated region with little intensive agriculture has probably contributed to the stability of these populations. An underlying historical trend toward cultural acidification (*e.g.*

Fritz *et al.* 1990) threatens their long-term security, but is outside the scope of current legislation and its effects are often hard to predict or detect. Sites in lowland Britain where *Luronium* populations are less stable must therefore be considered a priority for conservation.

Effective policies depend here on fully recognizing the crucial importance of controlled disturbance, often from artificial sources. This in itself will present a challenge to many conservationists. Meanwhile there are the parallel dangers of complacency arising from a belief that *Luronium* is still increasing and, paradoxically, from new legislation which will risk losses through an over-protectionist lack of disturbance. The decline or displacement of *Luronium* from a number of lowland SSSI's over the last 15 years, due to excessive disturbance or successional overgrowth of more competitive species in the absence of management, is a reminder that statutory protection alone does not guarantee survival.

The main management dilemma, therefore, is to create and maintain a disturbance regime which errs neither toward neglect nor toward excessive damage. On navigable canals, regulated, light recreational boat traffic may be the most effective means of providing low intensity disturbance, because direct physical intervention is not required. In steep-sided channels this is especially true, perhaps because reflective scour from boat-wash and an unfavorable bank profile suppress the establishment and overgrowth of reed swamp (notably *G. maxima*) and so retain an open marginal zone for less aggressive species. With this conservation strategy, *Luronium* can persist indefinitely at low abundance. Furthermore, water-plant communities then tend to be at their most species-rich and often contain additional species which are scarce in Britain, such as *P. trichoides* Cham. and Schlecht and *P. compressus*.

However, some prime canal habitats (*e.g.* Montgomery and Rochdale Canals) remain largely unnavigable. Natural infilling processes demand periodic channel dredging or control of emergent marginal vegetation to maintain water supply or land drainage functions, although these operations may also support a longer term objective of renewed navigation. Channel engineering works have inadvertently encouraged growth of *Luronium*, sometimes evident one or two seasons later as extensive monodominant stands. Without further intervention these populations are eventually displaced by more competitive elodeid species and reedswamp. Conservation by routine channel clearance may therefore offer an alternative to light boat traffic, but with less lasting results. Dredging must be repeated regularly to restore the open water phase and arrest succession. This could be on a rotational basis to provide a gradation of recovery states and accelerate recolonization from adjacent populated lengths.

Renewed boat traffic on restored canals presents a threat to *Luronium* if it exceeds critical levels. Sole reliance on the passive management effects of either low traffic or periodic channel clearance as outlined above may not be possible. The more difficult options of actively developing and managing offline refuges (BWB and NCC 1986), transplanting material, or regulating boat traffic on the main channel may have to be considered.

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