4 CANALS AS AQUATIC CORRIDORS

4.1 INTRODUCTION

The term 'corridor' can be used to describe two different situations. In the first, the corridor is simply a passage along which organisms travel, or along which propagules are dispersed. Thus, one can imagine a butterfly or a bird passing from one wood to another along a hedge, or a seed floating along a stream from one lake to another. The second situation is the corridor as a linear habitat in which organisms live and reproduce. This section of the report considers British canals as linear habitats for submerged and floating vascular plants.

A study of the plants which have colonized canals is of interest for two reasons. Canals are of intrinsic importance, as they contain significant populations of many scarce or rare aquatic macrophytes. They are unstable habitats: if neglected they gradually become overgrown by emergent vegetation but if maintained and intensively used by boat traffic they also lose much of their botanical diversity (Murphy & Eaton 1983). The restoration of canals for pleasure boating has been a controversial issue in recent years, and the management of the Basingstoke Canal, in particular, has been a subject of heated debate (see Byfield 1990). Proposals to use canals as part of a national water grid may also need to be evaluated by conservationists, and a knowledge of the dispersal behaviour and colonizing ability of both native and alien species will be essential if the consequences of linking canals are to be predicted.

4.2 REPRODUCTION AND DISPERSAL IN THE AQUATIC ENVIRONMENT

In considering aquatic corridors, an important feature of aquatic plants must be borne in mind: the prevalence of vegetative reproduction in many genera. Vegetative reproduction in British terrestrial species usually takes place simply by the growth of the parent individual. In many cases this is achieved by the growth of underground axes such as rhizomes, or of stolons close to the soil surface. Only a few species produce vegetative propagules which can combine the functions of dispersal and reproduction. These include those which produce specialized structures such as the bulbils of *Cardamine bulbifera* and *Saxifraga cernua* and the proliferous spikelets of viviparous grasses such as *Festuca vivipara* and *Poa bulbosa*. Less specialized propagules are rare: one example is the development of plantlets on the leaves of *Cardamine pratensis*. The only method of vegetative dispersal and reproduction which is at all frequent is seed apomixis, in which seeds are produced asexually.

By contrast, a wide range of vegetative propagules are produced by the relatively small number of aquatic macrophytes in the British flora. Floating species such as *Azolla filiculoides*, *Lemna* spp. and *Spirodela polyrhiza* reproduce simply by vegetative budding. Rooted macrophytes in other genera such as *Hydrilla*, *Myriophyllum* and *Potamogeton* may produce specialized turions derived from leafy tissue, whereas species of *Elodea*, *Groenlandia* and *Lagarosiphon* have less specialized branchlets which become detached from the parent plant and which are capable of regeneration. This capacity for vegetative reproduction is often accompanied by a failure to reproduce sexually: one or two apparently native species (eg. *Stratiotes aloides*) and several successful aliens (eg. *Elodea nuttallii*) are present in Britain as a single sex; some species rarely flower (eg. *Spirodela polyrhiza*) and others which do flower often fail to set viable seed (eg. *Hydrocharis morsus-ranae*). There are probably two reasons for the greater predominance of vegetative reproduction amongst aquatic plants. Drought is not a problem in the aquatic environment, and thus effective propagules do not need to have morphological features which protect them against desiccation. In this context it is interesting to note that a wide range of vegetative propagules is present in poikilohydric groups such as the bryophytes. Water is also an effective means of dispersal, and the propagules of plants in flowing water can be dispersed within the habitat in which they grow, rather than (as might, for example, be the case with wind dispersal) across hostile terrain.

4.3 THE GROWTH, DECLINE AND REVIVAL OF THE BRITISH CANAL NETWORK

Rivers have been important in the British transport system from prehistoric times. Attempts to improve rivers for navigation were made in the medieval period. Stretches of river which were particularly difficult to navigate were by-passed by cuts alongside the river. The improvement of the R Exe in 1564-67 was particularly significant as the cut which by-passed a stretch with shoals and weirs included three locks, the first time that these had been used in England. Further extensive river improvements took place in the 17th and 18th centuries. As river transport became more efficient, the inefficiency of transporting goods between rivers across their watersheds was increasingly apparent.

The start of the canal-building era can be dated from the construction of the Bridgewater Canal, which was authorized by Act of Parliament in 1760. This proved to be a financial success, and in the next 70 years many canals were built and a great many more planned but not started, or started and not completed. By 1830 there were over 4250 miles of navigable waterways, two-thirds of which were canals. The beginning of the railway era put an end to the period of canal construction. Some canals were actually sold to provide routes for railways and most suffered from competition from the railway network.

For over a century the canal network was in gradual decline. Although some canals remained viable, others lost all their traffic and became disused. Most of the remaining canals were taken into public ownership in 1948. There was no halt to the decline of the use of the network for industrial purposes, however. The nationally-owned fleet of narrow boats ceased operating in 1963, following losses caused by the 1962-63 winter.

The canals became increasingly important in the post-war years for recreational boating. Not only were existing canals used, but disused canals were restored using volunteer labour (the 'new navvies'). This revival has ensured the continued existence of many canals, but has at times brought the restoration movement into conflict with trade unionists and conservationists.

The distribution of canals in Britain and Ireland is given in Figure 4.1. Brief histories of the canal-building era, and details of the recent restoration projects, are provided by Baldwin & Burton (1983) and Squires (1984).

4.4 THE COLONIZATION OF CANALS BY AQUATIC MACROPHYTES

Aquatic macrophytes which have colonized canals have been identified using the Biological Records Centre (BRC) database. In recent years the data on aquatic plants held by BRC have been enhanced by the addition of records from a wide range of sources. This work has formed the basis of an Atlas and Database of Aquatic Plants project, jointly funded by ITE, the Joint Nature Conservation Committee and the National Rivers Authority (Preston, Croft & Forrest 1991; Preston & Croft 1992). As part of this project, data from specific canal surveys have been added to the database. Most of the canal surveys to which we have had access have concerned canals at the fringe of the national network, presumably because canals are more highly valued as a resource in areas where they are scarce than in areas where they are plentiful. Records from surveys of the following canals are now available in the database: Basingstoke Canal (Hall 1988), Chesterfield Canal (Alder 1986), Exeter Canal (C.D. Preston unpublished), Forth & Clyde Canal (Watson & Murphy 1988), Grand Western Canal (B. Benfield & L.J. Margetts unpublished), Grantham Canal (Candlish 1975), Lancaster Canal (Livermore & Livermore 1988), Leven Canal (Kendall 1987), Pocklington Canal (Tolhurst 1987) and Union Canal (Anderson & Murphy 1987). Other records from canals have come from datasets which have contained records from various habitats. These are detailed by Preston & Croft (1992).

Aquatic macrophytes for which there are records in canals from at least 10 of the 10 × 10km squares of the national grid are listed in Table 4.1 This cut-off point of 10 squares has been chosen to select those species which are well established in canals, and eliminate those which have only been recorded as casual occurences in canals or which have become established only in a few short stretches of canal. We have also attempted to identify those species which have failed to colonize the canal system to any significant extent. Species which have been recorded from at least 100 10-km squares in Britain, but have not been recorded from canals in more than 9 of them, are listed in Table 4.2 It does not seem worth listing the rarer species which have failed to colonize canals, as their opportunity to do so might have been very limited.

4.5 BIOLOGICAL CHARACTERISTICS OF CANAL COLONISTS

The biological characteristics of the canal colonists can be compared with those of the species which have failed to colonize canals in an attempt to identify features which correlate with colonizing ability. The characters which are examined here are British distribution, life form, method of reproduction and trophic requirements.

Figure 4.1 The distribution of canals in Britain and Ireland. Solid circles denote the presence of a canal in the relevant 10-km square; open circles are the sites of former canals which are now dry.

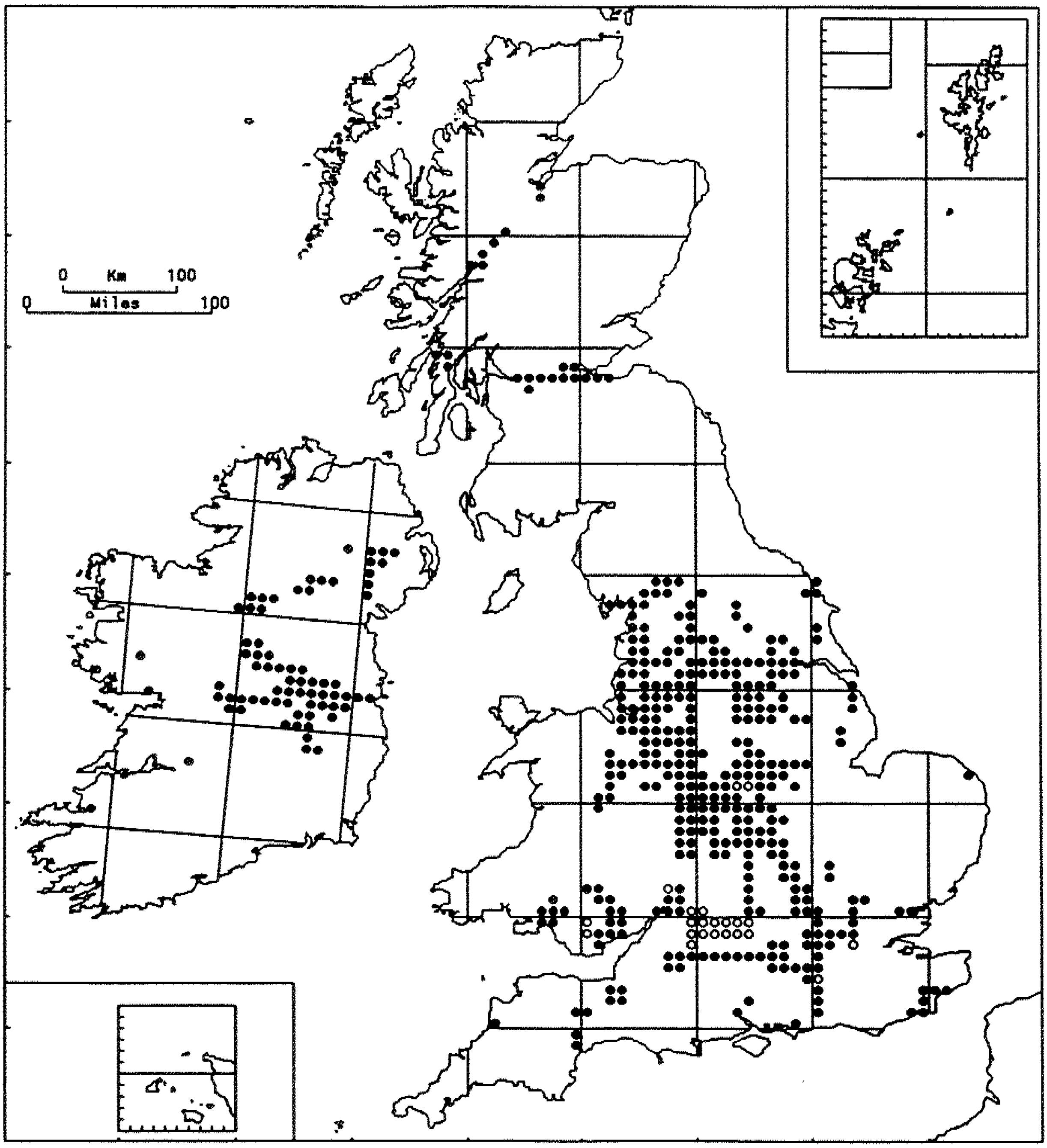

Table 4.1 Submerged and floating vascular plants recorded from canals in 10 or more 10-km squares in Britain

- *Apium inundatum*
- * *Azolla filiculoides*
- *Callitriche hamulata*
- *Callitriche hermaphroditica*
- *Callitriche platycarpa*
- *Callitriche stagnalis*
- *Ceratophyllum demersum*
- *Eleocharis acicularis*
- * *Elodea canadensis*
- * *Elodea nuttallii*
- *Groenlandia densa*
- *Hippuris vulgaris*
- *Hydrocharis morsus-ranae*
- *Lemna gibba*
- *Lemna minor*
- *Lemna trisulca*
- *Luronium natans*
- *Myriophyllum spicatum*
- *Myriophyllum verticillatum*
- *Nuphar lutea*
- *Nymphaea alba*
- *Nymphoides peltata*
- *Oenanthe fluviatilis*
- *Polygonum amphibium*
- *Potamogeton alpinus*
- *Potamogeton berchtoldii*
- *Potamogeton compressus*
- *Potamogeton crispus*
- *Potamogeton friesii*
- *Potamogeton lucens*
- *Potamogeton natans*
- *Potamogeton obtusifolius*
- *Potamogeton pectinatus*
- *Potamogeton perfoliatus*
- *Potamogeton praelongus*
- *Potamogeton pusillus*
- *Potamogeton trichoides*
- *Potamogeton* x *cooperi* (*P. crispus* x *perfoliatus*)
- *Potamogeton* x *lintonii* (*P. crispus* x *friesii*)
- *Potamogeton* x *salicifolius* (*P. lucens* x *perfoliatus*)
- *Ranunculus circinatus*
- *Sagittaria sagittifolia*
- *Sparganium emersum*
- *Spirodela polyrhiza*
- *Stratiotes aloides*
- *Zannichellia palustris*

* denotes an introduced species

Table 4.2 Submerged and floating vascular plants recorded from over 100 10-km squares in Britain but recorded in canals from fewer than 10 10-km squares

Callitriche brutia
Callitriche obtusangula
Ceratophyllum submersum
Crassula helmsii
Elatine hexandra
Eleogiton fluitans
Hottonia palustris
Isoetes echinospora
Isoetes lacustris
Juncus bulbosus (aquatic form)
* *Lagarosiphon major*
Littorella uniflora
Lobelia dortmanna
Myriophyllum alterniflorum
Potamogeton coloratus
Potamogeton filiformis
Potamogeton gramineus
Potamogeton polygonifolius
Potamogeton x *nitens* (*P. gramineus* x *perfoliatus*)
Ranunculus aquatilis
Ranunculus baudotii
Ranunculus fluitans
Ranunculus peltatus
Ranunculus penicillatus subsp. *pseudofluitans*
Ranunculus trichophyllus
Ruppia cirrhosa
Ruppia maritima
Sparganium angustifolium
Subularia aquatica
Utricularia intermedia sens. lat.
Utricularia minor
Utricularia vulgaris

* denotes an introduced species

4.5.1 British distribution

The aquatic macrophytes can be classified into six groups on the basis of their British distribution. **Widespread** species are found throughout much of Britain whereas **coastal** species are confined to the coastal zone. **Strongly south-eastern** species are virtually confined to the southern and eastern part of Britain, being rare in SW England, Wales, N England and Scotland. **Weakly south-eastern** species are concentrated in the same area but also extend further north and west, and are often present in lowland Scotland, Orkney and the Outer Hebrides. **Strongly north-western** species are virtually confined to western Scotland, NW England and Wales; **weakly north-western** species occur predominantly in these areas. Although these categories are somewhat arbitrary, most of the species under consideration can be assigned without difficulty to a category by visual inspection of the distribution maps prepared by Preston, Croft & Forrest (1991). Only a few have anomalous distributions which makes their placement in any group rather unsatisfactory; these have been allocated to the least unsatisfactory category.

The distribution of canal colonists and non-colonists is shown in Table 4.3. The majority of widespread and south-eastern species have colonized canals (44 species), although a significant minority (15 species) have failed to do so. Only two weakly north-western species and none of the strongly north-western or coastal species appear in the list of colonists.

Table 4.3 The British distribution of canal colonists and non-colonists

British distribution	Colonists	Non-colonists	Total
Strongly south-eastern	18	7	25
Widespread	16	4	20
Weakly south-eastern	10	4	14
Weakly north-western	2	7	9
Strongly north-western	0	7	7
Coastal	0	3	3
Total	46	32	78

4.5.2 Life-form

The colonists and non-colonists have been allocated to the following life-form classes:

1 free-floating
2 rooted; submerged leaves capillary; floating leaves absent
3 rooted; submerged leaves capillary; floating leaves present
4 rooted; submerged leaves linear; floating leaves absent
5 rooted; submerged leaves linear; floating leaves present
6 rooted; submerged leaves broad; floating leaves absent
7 rooted; submerged leaves broad; floating leaves present
8 rooted; submerged leaves absent; floating leaves present
9 plants capable of growth and reproduction in terrestrial habitats.

The first eight categories are mutually exclusive but plants from any of them could potentially also grow terrestrially, and hence belong to the ninth. The capacity to produce floating leaves is the relevant attribute in deciding between 'floating leaves present' and 'floating leaves absent'; individual plants or populations may produce floating leaves only in particular environmental conditions.

The life-forms of colonists and non-colonists are shown in Table 4.4. The most significant features of the table are the fact that all free-floating species present in more than 100 10-km squares in Britain have colonized canals. The broader the submerged leaves of a species the higher the chance that it is a colonist: 71% of the broad-leaved species have colonized canals compared to 62% of linear-leaved species and 33% of capillary-leaved plants. There is no suggestion that a capacity to grow terrestrially favours colonization.

Table 4.4 The life-form of canal colonists and non-colonists

Life-form	Colonists	Non-colonists	Total
Free-floating	7	0	7
Rooted, submerged leaves capillary,			
without floating leaves	7	13	20
with floating leaves	1	3	4
subtotal	8	16	24
Rooted, submerged leaves linear,			
without floating leaves	6	5	11
with floating leaves	7	3	10
subtotal	13	8	21
Rooted, submerged leaves broad,			
without floating leaves	12	2	14
with floating leaves	3	4	7
subtotal	15	6	21
Rooted without submerged leaves	3	0	3
Capable of growth and reproduction in terrestrial habitats	2	6	8
Total	48	36	84

4.5.3 Method of reproduction

The methods of reproduction of the colonists and non-colonists are summarised in Table 4.5. Vegetative reproduction is considered separately from sexual reproduction. Three categories of vegetative reproduction are recognised: free-floating species which reproduce by budding, species which regularly produce specialized propagules and species which occasionally produce such propagules. Most of the species with one of these forms of reproduction have colonized canals. The fact that the free-floating species are all colonists has already been noted. Of the species with specialized propagules, 14 are colonists whereas only three are not. There are, of course, other forms of vegetative reproduction. In particular, plants may become established from pieces which become detached or from entire plants which are uprooted and washed away. It is, however, impossible to estimate the extent to which such fragments or plants will become established on the basis of existing information.

Table 4.5 The methods of reproduction of canal colonists and non-colonists

Method of reproduction	Colonists	Non-colonists	Total
Vegetative reproduction			
Free-floating species; reproducing by budding	7	0	7
Specialized propagules frequently produced	12	3	15
Specialized propagules occasionally produced	2	0	2
No specialized propagules	26	29	55
Sexual reproduction			
Seed regularly produced	31	24	55
Seed occasionally produced	3	5	8
Seed rarely or never produced	10	3	13
Total	91	64	155

The species have also been divided into three categories according to the frequency with which they produce seeds: plants which regularly bear seed have been distinguished from those which only occasionally seed and those which rarely if ever set seed. No marked differences between colonists and non-colonists are apparent, and there is no suggestion that capacity to produce seed favours colonization.

Six of the species listed lack specialized means of vegetative dispersal and never set seed. Three of these have colonized canals and three have not.

4.5.4 Trophic requirements

A 'trophic ranking score' for many of the species listed in tables 1 and 2 is provided by Palmer, Bell & Butterfield (1992). Scores range from 2.5 to 10. Species with a low score are characteristic of nutrient-poor waters whereas those with high scores are strongly associated with eutrophic sites. The mean score for the canal colonists is 8.5, whereas that for the non-colonists is 6.1. Sixteen colonists and 12 non-colonists have been excluded from this analysis as a score is not available for them.

The above discussion of individual attributes has identified a number of features which are characteristic of colonists. These may not all be directly related to colonizing ability: the fact that most colonists are southern species would lead one to expect that the colonists would have a higher trophic ranking score than the non-colonists. The following features of colonists emerge most strongly from the analysis: they are predominantly southern or widespread species (not unexpectedly, in view of the distribution of canals), broad-leaved species are much more likely to colonize than capillary-leaved species and the presence of specialized forms of vegetative reproduction favours colonization whereas reproduction by seed is of little significance. These are only generalisations, however, and it should be noted that the alien *Elodea nuttallii*, which does not produce seed in Britain (the species is dioecious and only female plants are present here) and lacks specialized vegetative propagules, has nevertheless become established in canals and in many other British water bodies in recent years.

It is hard, on the basis of British distributions, to distinguish between trophic and climatic preferences. The geographic tendencies noted in Section 4.5.1 are probably more the result of the distribution of eutrophic waters than of a preference for warmer climates.

4.6 TAXA WITH A HIGH PROPORTION OF THEIR POPULATIONS IN CANALS

A number of species have a high proportion of their populations in canals. These include some of the species listed as canal colonists in Table 4.6 and others which are too rare to be included in that table. A list of the species recorded from canals (although sometimes also present in other habitats) in at least 30% of the 10-km squares in which they are recorded nationally is provided in Table 4.6.

The species listed in Table 4.6 can be divided into three groups. The largest is a group of seven rare aliens which have become established in a few canals. *Potamogeton epihydrus* can also be considered to be a member of this group as it is established as an alien in canal sites in N. England, although native in the Outer

Hebrides. Some of the aliens are (or were) found in canals which received warm water from adjacent industrial sites (eg. *Egeria densa*, *Najas graminea*).

The second group of species in Table 4.6 are native and grow in natural habitats, but have nevertheless spread into the canal system to such an extent that these populations account for a significant proportion of their British occurrences. In S. England *Potamogeton compressus*, *P. friesii* and *P. trichoides* are plants of slowly flowing lowland rivers and drainage ditches, and presumably spread from these habitats into canals. All three reproduce by turions and by seed, the former probably being the normal method of reproduction in canals. *Luronium natans* is a native of lakes in Wales and the adjacent English counties. It occurs in lakes in Shropshire alongside the Shropshire Union Canal, and appears to have spread along the canal network south-westward into the Montgomeryshire Canal and north-eastward into the canals of N. England (Figure 4.2).

The third group of species in Table 4.6 are four sterile *Potamogeton* hybrids. Three of these are hybrids of *P. crispus* and like that species reproduce by turions. The fourth, *P.* × *salicifolius* has no specialized means of vegetative reproduction.

Table 4.6 Submerged and floating vascular plants recorded in canals in less than 10 10-km squares, but found in canals in at least half of the 10-km squares in which they occur

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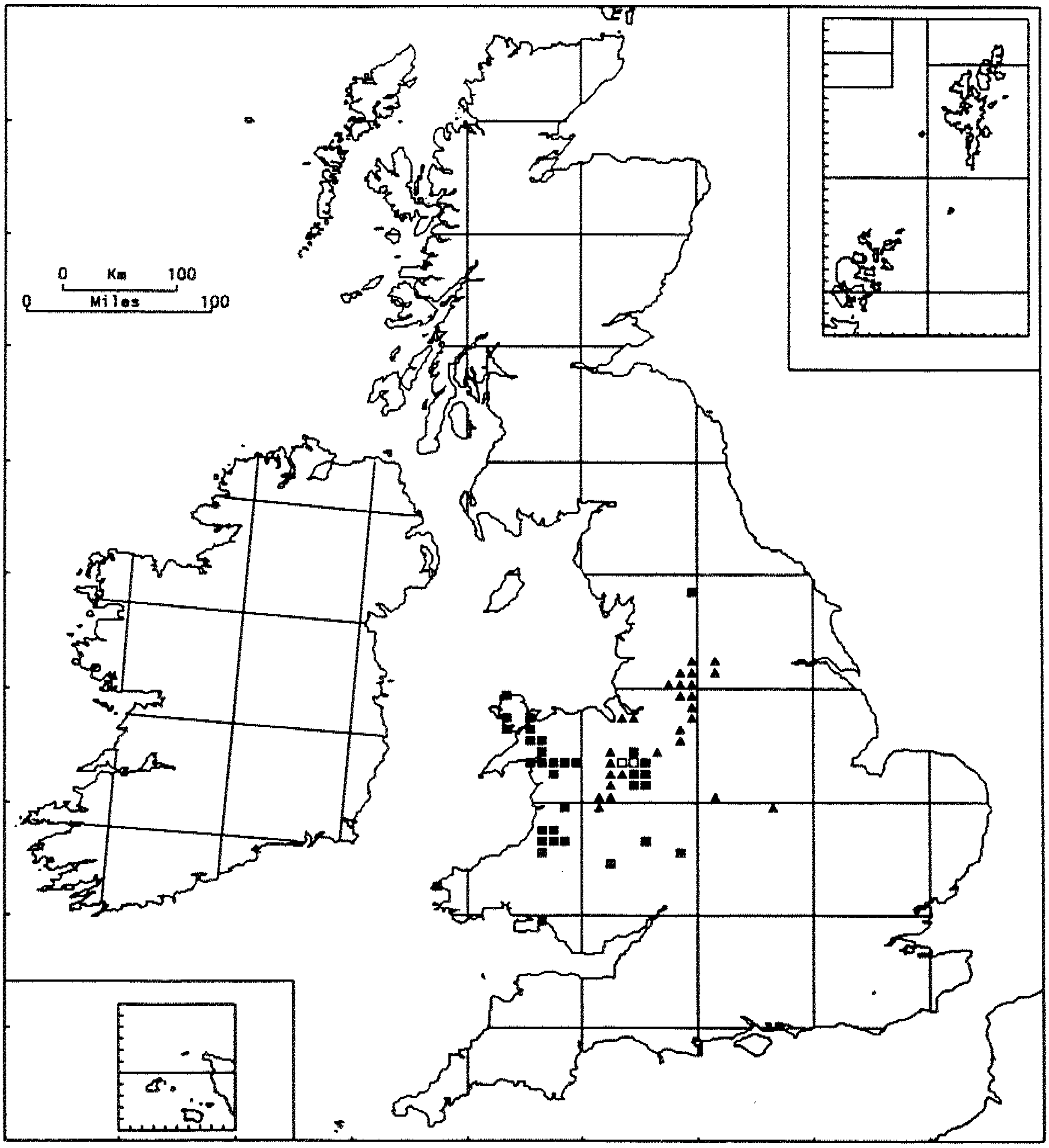
* *Egeria densa*
* *Elodea callitrichoides*
* *Luronium natans*
* *Myriophyllum heterophyllum*
* *Najas graminea*
Potamogeton x *bennettii* (*P. crispus* x *trichoides*)
Potamogetom compressus
Potamogeton x *cooperi*
Potamogeton epihydrus
Potamogeton friesii
Potamogeton x *lintonii*
Potamogeton x *salicifolius*
Potamogeton trichoides
Sagittaria rigida
* *Vallisneria spiralis*

---

* denotes an introduced species

Figure 4.2 The distribution of *Luronium natans* in native habitats (solid squares) and canals (triangles). Squares in which the species grows in both habitats are shown as open squares. Squares where the plant has been introduced to other habitats are omitted.



4.7 TAXA CONFINED TO PARTICULAR CANAL SYSTEMS

A number of taxa are confined to particular canal systems, or occur in particular canals well outside of their normal range. These illustrate the existence of effective barriers to dispersal in some aquatics. The extreme example is *Potamogeton × bennettii*. This hybrid between *P. crispus* and *P. trichoides* was first found in wood ponds at Grangemouth in 1890. These ponds were at the east end of the Forth and Clyde Canal, and were used for seasoning timber. The hybrid survived in the wood ponds until at least 1937, but the ponds have since been drained and built over. However, *P. × bennettii* was found in the Canal itself in 1960, and is now known to be well established in the western end of the canal (Figure 4.3). It has not been found anywhere else in the world. It is difficult to believe that the environment of the Forth & Clyde Canal is in any way special, and the only plausible explanation for the restriction of *P. × bennettii* to this canal is its inability to spread to other waters.

Two species can be mentioned as examples of plants which are confined to particular canals outside their native range. *Potamogeton epihydrus* is a widespread species in N. America but in Europe is only found as a native in the Outer Hebrides. It has, however, been established as an alien (of unknown origin) in the Calder & Hebble Navigation and in the Rochdale Canal (Figure 4.4). It is again difficult to explain this restriction in ecological terms. *Lemna gibba* is widespread in S. England but confined in Scotland to the Forth & Clyde and Union Canals (Figure 4.5). In this case it is possible that ecological factors restrict the distribution of this species in Scotland. These examples contrast with the ability of some aquatics to spread into isolated waters.

4.8 THE POSSIBLE CONSEQUENCES OF LINKING CANALS AS A WATER GRID

This brief review has highlighted some of the features that characterise colonists, and a more sophisticated statistical analysis of the data presented here might clarify these trends. The mobility of many aquatic species is demonstrated by the fact that 44 of the 59 submerged and floating species with a widespread or southerly distribution in Britain have colonized the canal network. However, some macrophytes are apparently restricted to particular canals or canal systems by an inability to spread. These include scarce native species and aliens which have not (yet?) become widely established. Some of these might be expected to spread into a water grid if the canals in which they grew were connected to it.

4.9 CONCLUSIONS

1. Many aquatic plants are highly mobile.

2. Dispersal of vegetative propagules is much more important in the aquatic than the terrestrial environment.

3. Colonists of canals in Britain have been species which are widespread or have a southerly distribution; coastal and northern species are not established to any significant extent. Colonists tend to have linear or broad rather than capillary leaves.

4. Despite the general mobility of aquatic species, there is evidence that some taxa are restricted to particular canal systems because of an inability to reach other sites.

5. The linking of canals as a national grid might facilitate the spread of some alien macrophytes.

Figure 4.3 The British (and world) distribution of *Potamogeton* × *bennettii*. Closed circles denote records made in or after 1950; open circles, earlier records.

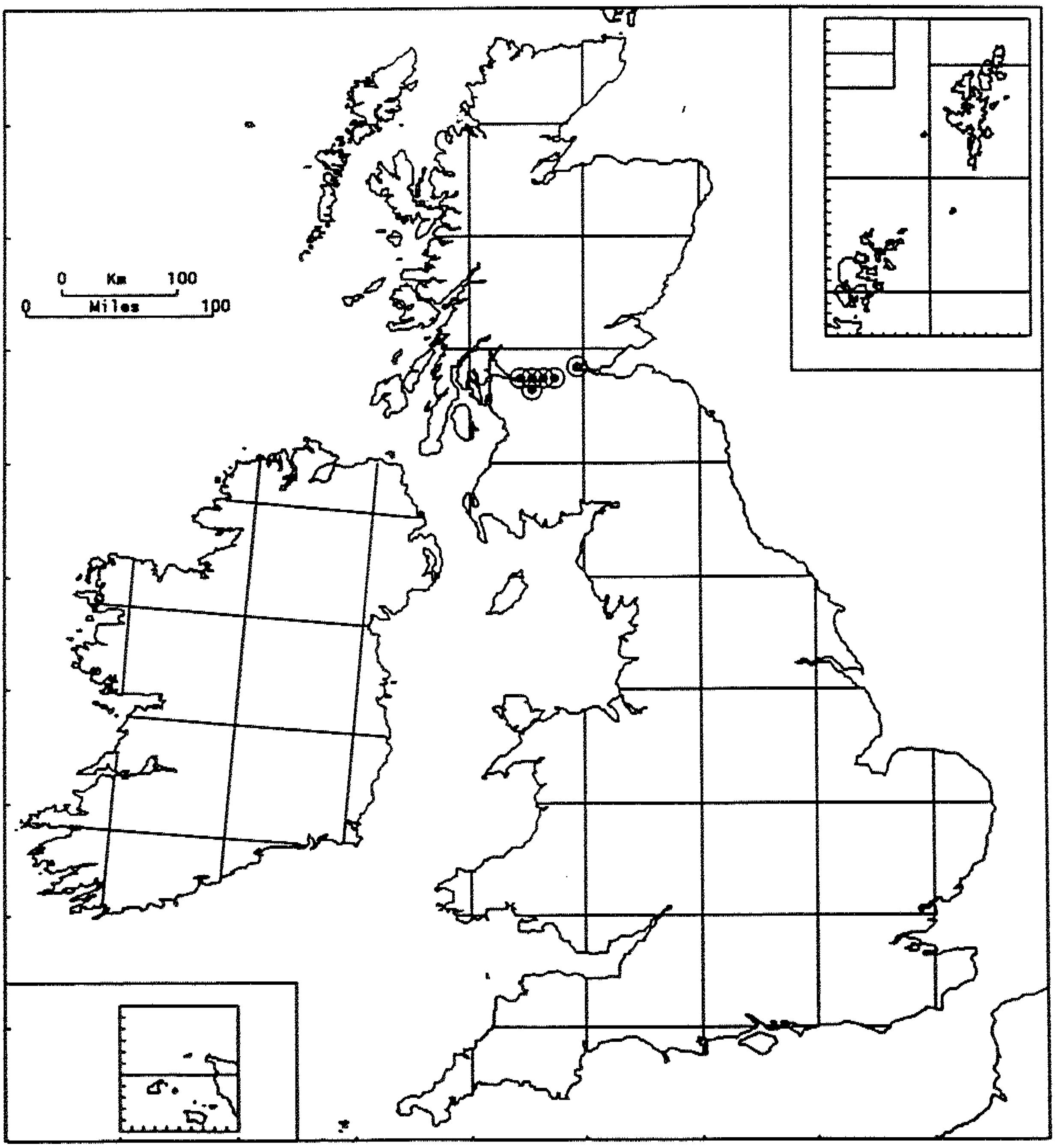


Figure 4.4 The British distribution of *Potamogeton epihydrus*. Closed circles denote records made in or after 1950; open circles, earlier records.

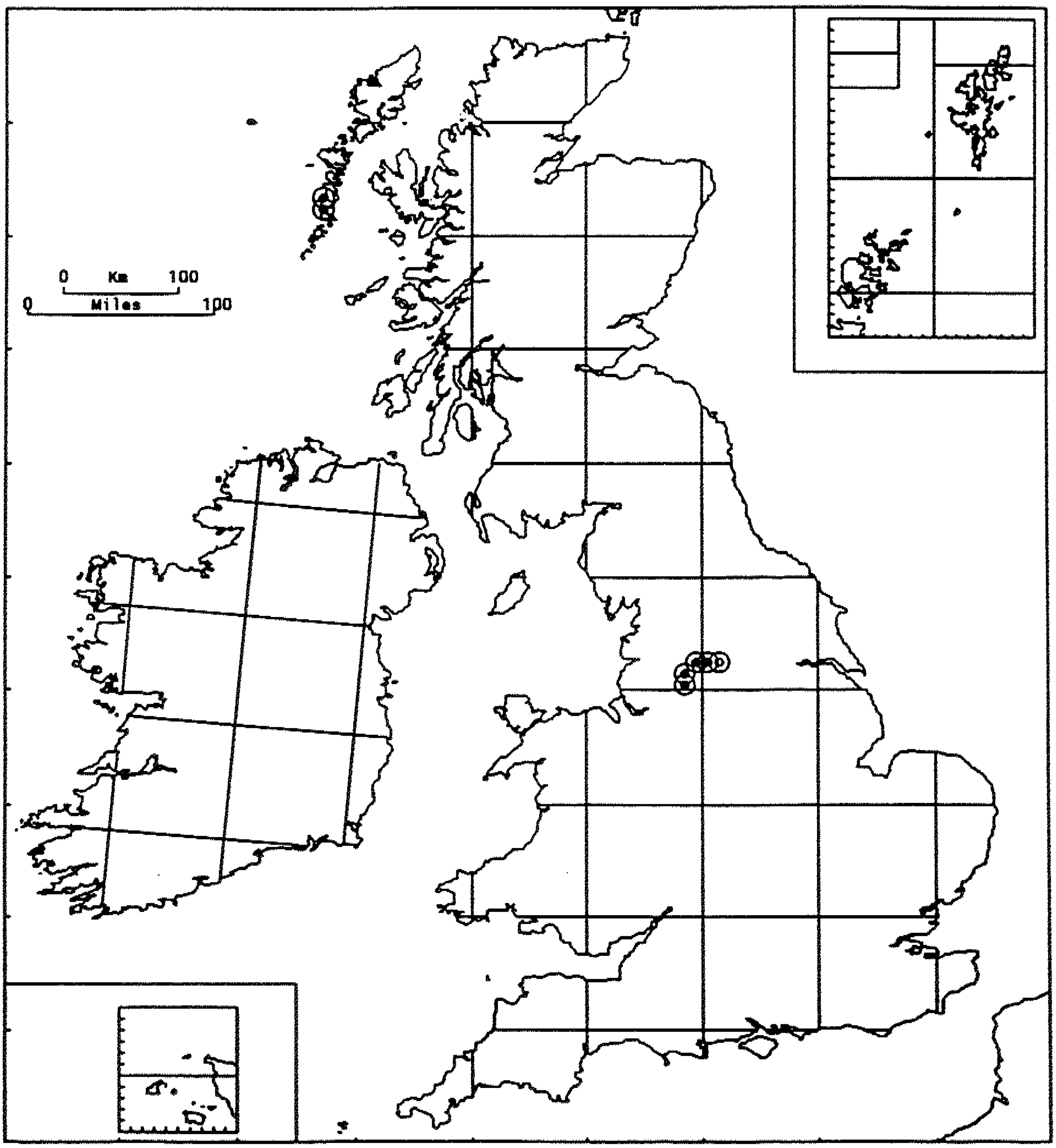
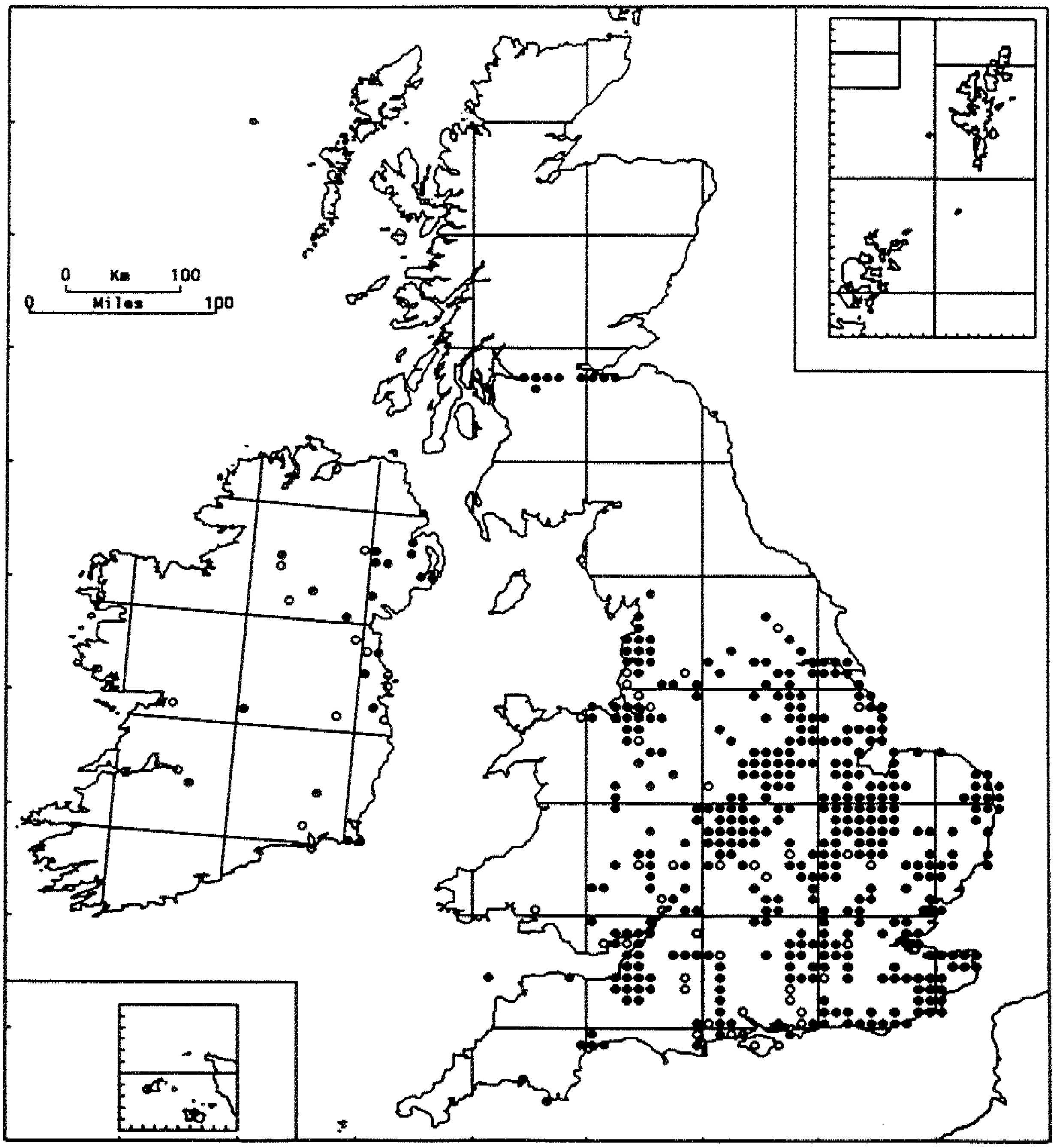


Figure 4.5 The British distribution of *Lemna gibba*. Closed circles denote records made in or after 1950; open circles, earlier records.



5 METAPOPULATION DYNAMICS IN PATCHY HABITATS

G W Elmes, R C Welch & P D Carey

5 METAPOPULATION DYNAMICS IN PATCHY HABITATS

5.1 INTRODUCTION

A great deal has been written on metapopulation dynamics but there is relatively little hard information for invertebrates or plants. The problem is essentially one of dispersal confounded by fractal geometry, eg. most invertebrates live at and perceive their world on a different scale to most vertebrates. Vertebrates are usually about the same order of magnitude of size as ourselves, and have sensory systems similar to ourselves, therefore our perception of the world can more easily be extrapolated to these animals.

All natural environments have a grain or patchiness (Harper 1980, Rolstad 1991). We can therefore consider the environment as a mosaic of habitable sites for any particular species (Gadgil 1971). Different species will, however, interpret the patchiness of the environment on different scales (Harper 1980). Spotted owls move around in a patchy landscape which covers hundreds of hectares with habitable sites being tens of hectares across (Gutiérrez & Carey 1985) whereas a woodlouse sees the world in terms of metres with habitable sites centimetres across. If we are to investigate the way species move around the landscape we should consider the distance between habitable sites on a scale which is based on the dispersal characteristics of that species (Harper 1980, Levin 1981, Howe & Westley 1986), not on the anthropocentric scales of the kilometre or centimetre.

5.1.1 Living in a patchy world

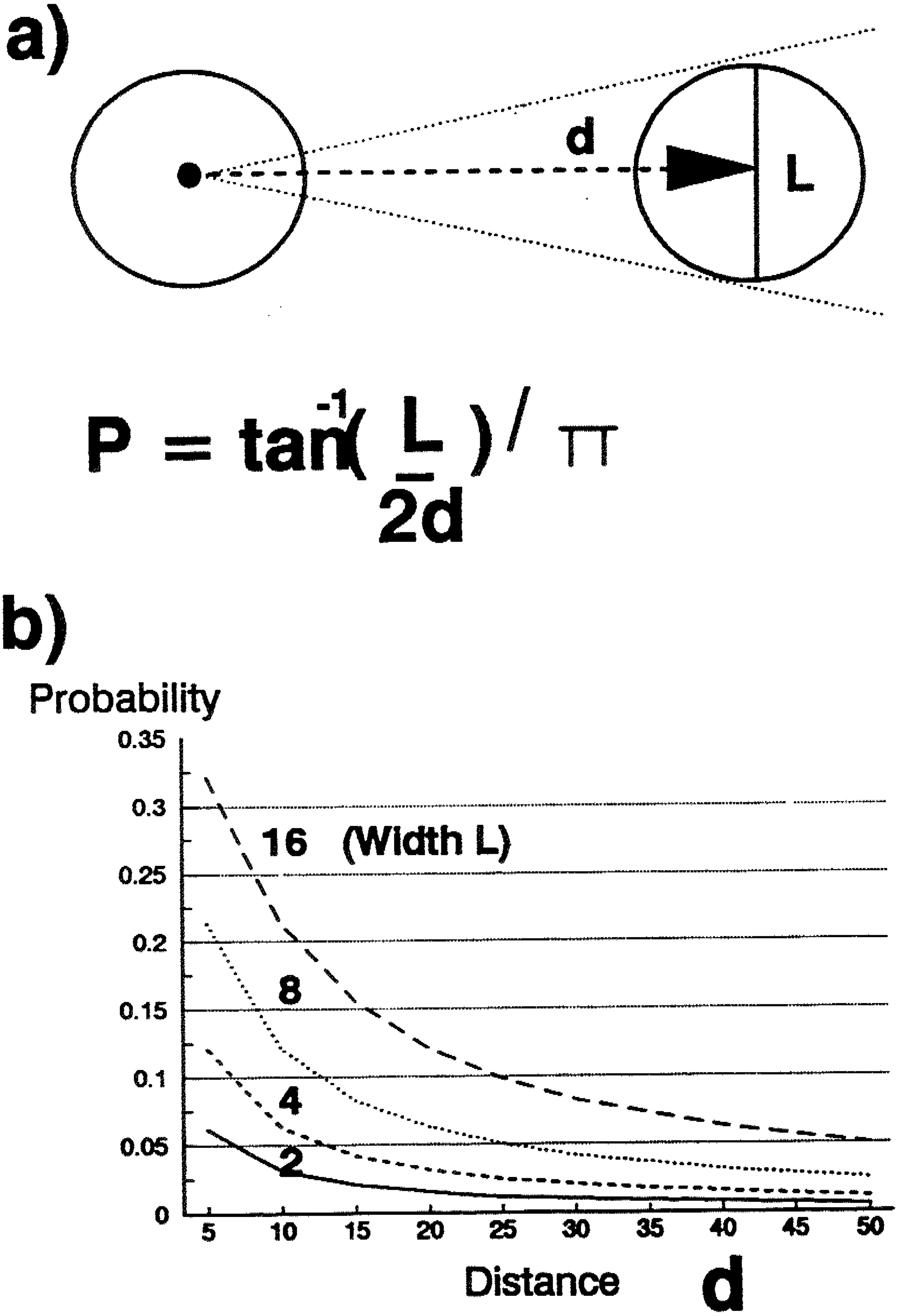
For simplicity in this section we will consider how animals move around the landscape, many of the arguments are the same for plants but they require that stress is placed on the fact that plants are moved and do not move.

The general problem of moving between patches of suitable habitat is summarized in Figure 5.1a. Take two ecosystems, A and B, that contain suitable habitat of an animal and are separated by areas that contain no suitable habitat. What is the probability that a mobile individual leaving patch A in a random direction will encounter patch B ? For any individual, there will be a maximum distance that it can disperse before it expires. If the distance A from B is within that limit, then the probability (P) is:

$$P = \tan^{-1} (L/2d) / \pi \qquad \ldots\ldots 5.1.$$

(calculated in radians) where L is the diameter (or width normal to the direction from A) of patch B and d is the distance between the centres of patches. From this it is obvious that P varies directly with L and inversely with d (Figure 5.1b). As L increases $P \rightarrow 0.5$, in other words, even with a relatively enormous patch B, the animal must move in that general direction to encounter it.

Figure 5.1 The probability of an animal moving from patch A to patch B.



$$P = \tan^{-1}\left(\frac{L}{2d}\right) / \pi$$

Two other variables will modify P. First, bias in the direction in which animals leave patch A. This may be active, for example animals may always start dispersing uphill, or passive, for example animals that disperse on the wind will be biased towards the direction of the prevailing winds. Secondly, P will be modified in some way by the animal's ability to survive the journey *d* over, in or through inhospitable habitat. In the case of active dispersal this will be some combination of the animal's individual characteristics and the 'hostility' (θ) of the interpatch habitat, so that P (in Equation 5.1) will be modified by $1/d^*\theta$. Survival of passive dispersers (air and water borne animals) might be more dependent on other factors such as windspeed rather than distance.

If an animal reaches the new ecosystem B, it might encounter others of its own kind and become part of the breeding population supported by B. If it is the first of its kind then it has to be able to originate a new population (with invertebrates, this means in practice that it must be a gravid female or a parthenogenetically reproductive individual). It is in this respect that patch theory and the theory of island biogeography (McArthur & Wilson 1967) overlap.

5.1.2 Island biogeography

In the classic theory of island biogeography, the ecosystems B would be a new, sterile piece of land, separated from mainland A by sea. The probability of a dispersing animal finding B is inversely proportional to the distance *d* (as above) but its chances of surviving on the new island depends upon its encountering its habitat once there. These will be greater the longer an island has been in existence and greater on big islands that are more likely to have biotopic diversity compared to small ones.

There has been much interest in the evolution of natural communities under such circumstances. The hypothesis of island biogeography is that on islands that have been in existence for a long time, the net result of separate species colonization events should produce a biological (species) diversity that varies inversely with the distance from the mainland source of colonizers and directly with the island's area.

The first tests on island faunas showed that this relationship usually held true, but was not always a very good predictor of species diversity on islands. To explain these discrepancies the theory has been adjusted to take account of larger islands acting as "mainlands" for satellite islands and nearer islands acting as "mainlands" for more distant ones. In this respect the concepts approach and merge with the theory of patchy habitat and metapopulations (Gilpin & Hanski 1991).

5.1.3 Metapopulation dynamics theory

The concept of how populations interact was introduced in the theory of island biogeography (MacArthur & Wilson 1967). Levins (1970) introduced the idea that populations of populations exist and these "metapopulations" have dynamics of their own. In recent years there have been considerable developments in the theory of metapopulation dynamics (see Gilpin & Hanski 1991). The definitions given by

Hanski & Gilpin (1991) of describing populations , metapopulations and geographic distribution are:

Local scale - The scale at which individuals move and interact with each other in the course of their routine feeding and breeding activities.

Metapopulation scale - The scale at which individuals infrequently move from one place to another, typically across habitat types that are not suitable for their feeding and breeding activities, and often with substantial risk of failing to locate another habitable site.

Geographic scale - the scale of species' entire geographic distribution; individuals have typically no possibility of moving to most parts of the range.

Current metapopulation-dynamic models are almost without exception applied to animals (but see Carter & Prince 1981). All metapopulation models stem from Levins' simple model (Equation 3.1) based on a single species in temporally changing environments. It is clear that the key factors of metapopulation dynamics are extinction and colonization. There is obviously a very close link, therefore, between metapopulation dynamics and island biogeography (MacArthur & Wilson 1967). The main difference between the two approaches is that in island biogeography models there is a large mainland which is immune to extinction and is not affected by the island populations whereas in metapopulation dynamics models all populations can go extinct and can be affected by neighbouring populations.

5.1.4 Sources and sinks

Most metapopulations in the real world are likely to show behaviour which is intermediate between the Levins model and the mainland-island model (Hanski & Gilpin 1991) where large "core" populations can produce and support a large number of "satellite" populations (Harrison *et al.* 1988; Harrison 1991). The core and satellite population structure should not be confused with the "source - sink" structure. In the latter, populations in less favourable habitats, sinks, are maintained by constant immigration of individuals which come from sites where there is a surfeit of individuals, sources (Watkinson 1985). If the source "dries up" the sink will head towards extinction. Unlike core-satellite populations the source populations need not be larger than the sink populations and often they are not (Pulliam 1988).

5.1.5 Isolation and size of habitable sites

Two of the major generalities that result from both metapopulation dynamics and island biogeography are that the extinction rate decreases with increasing area of habitable sites, and the colonization rate decreases with increasing isolation (MacArthur & Wilson 1967; see Hanski 1991 for numerical references). These generalities enable us to relate current or even future landscapes to the survival and persistence of metapopualtions created by the fragmentation of habitat. The Levins model, for example, predicts that systems of small habitable sites, or systems in which the degree of isolation is great may not maintain metapopulations but can probably offer only temporary support to local populations. Unless the regional persistence of species is ensured by large, more or less permanent source populations (Boorman & Levitt 1973, Schoener & Spiller 1987, Harrison, Murphy & Ehrlich 1988), the colonization ability of a species will be crucial to its survival in a fragmented habitat (Ebenhard 1991). So species with limited colonizing ability will in many cases not form self supporting metapopulations from fragmented larger populations.

5.2 METAPOPULATION DYNAMICS THEORY AND INVERTEBRATES

For invertebrates, the distinction between ecosystems, biotopes and habitats must be appreciated. Ecosystem and biotope define the natural world from man's perspective; a biotope is defined by a recognizable combination of physical conditions and plant species. The biotope appropriate to a species may be present without any available habitat.

The habitat of most invertebrate species, particularly many rare ones, is poorly known and, being a mental construct, is difficult to map. What can be mapped for the "better known" species is actual and potential range. Also, for many species, distributional records can be used to list the biotopes from which a species has been recorded (see Chapter 6). The relative abundance of the records gives some indication of the biotopes most likely to provide habitat for the species. Biotopes, though an imprecise concept can be and have been, mapped. Therefore scientists often work with biotopes rather than directly with the species' habitat and tend to think in terms of areas of "good" biotope linked by corridors of "poorer" biotope.

This can cause difficulties. Take for an example heather moorlands, an easily recognizable biotope that most people are familiar with. On a coarse scale of resolution this biotope occurs in 3 regions of Southern England (Figure 5.2A), each having rather different characteristics resulting from local climate and geology. Consider a hypothetical heathland specialist invertebrate species, restricted to Southern England by limits of climatic tolerance. If the species can disperse large distances then it might exist in England as a single large metapopulation, whose habitat distribution is coincident with the distribution of heathland biotope. Such a population would probably be simply part of a larger population distributed on heathland throughout southwest Europe.

However, if individual dispersal is limited then patches of biotope could be linked, for example the range of dispersal indicated in Figure 5.2B might result in seven or eight isolated populations, each with a metapopulation structure dependent upon several patches of heathland. However, if dispersal is sufficiently poor to restrict the hypothetical species to major patches, the situation does not become much simpler. Each major patch, when viewed at a finer scale consists of many smaller patches (eg. the South Dorset heaths, Figure 5.3A). A detailed study would probably show that the species consisted of several sub populations each with a metapopulation structure.