

Draft Project Report

R&D Project 291

Riparian and Instream
Species-Habitat Relationships

University of Leicester
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ENVIRONMENT AGENCY



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FOREWORD

The authors of this report wish to express their thanks to members of the Project Steering Group – Richard Howell (Project Leader), Peter Barham, John Hogger and Paul Raven – for advice and encouragement throughout.

Many NRA regional staff assisted in the early stages with advice and suggestions. Conservation organisations and University / Polytechnic biology departments were mailed or visited with a request for relevant unpublished research; and we are grateful to the majority who responded positively.

Members of the M.Sc. Natural Resources Management course (1991-92) at Leicester University carried out some of the species-orientated literature reviews as part of their course-work. Debbie Kemp-McCarthy also helped with parts of the literature search which concerned her work on riparian vegetation.

SUMMARY

1. This Project Report supplements information contained in the R&D Report of NRA R&D Project 291. A 'Surveyors Handbook' is appended to that report.
2. The biological value of river corridor habitats has been identified by literature review following consultation with NRA Conservation Officers and some conservation bodies.
3. The bulk of the literature dealt with individual species and their habitat requirements. Fifty-three species, chosen as a result of the consultation process, were reviewed.
4. A smaller proportion of available literature dealt directly with habitats and their use by species assemblages.
5. The species-orientated information is presented for each species in turn: as a habitat summary listing key requirements; a distribution map; and a short prose review.
6. The habitat-orientated information is presented in this report as a sequential prose review. One-paragraph summaries for each of thirty habitats, selected as ecologically and visually distinct, are provided in the Handbook.
7. A recommended River Corridor Survey sheet was constructed for the Handbook. This was based upon the original NCC methodology and supplemented by the results of the current review. Habitats and species are cross-referenced on the survey sheet.
8. The project was primarily limited by its duration, set against the turn-round time of obtaining literature items and regionally-held information. In this context, and from the information collected, there are three main areas which would benefit from additional work:
 - Species review: more attention to terrestrial species which utilise riparian corridors, and to invertebrate species.
 - Habitat review: greater emphasis upon fragmented terrestrial habitats (such as hedgerows and other linear artificial corridors) would have given firmer support for the final riparian habitat selection.
 - RCS information is rarely collated for use in a wider context. This project could not try to draw out the considerable information in such surveys; but the NRA has now initiated a major R&D project towards that goal.

RECOMMENDATIONS

The following recommendations are made to advance the scientific basis and application of River Corridor Surveys:

1. RCS should be carried out to a restricted number of clearly defined levels of intensity (not more than three) for different purposes.
2. A central, or at least regional, database should be established to summarise the results of RCS, particularly at the high levels of intensity; and this database should be capable of comparative analysis.
3. This review, if found useful, should be extended to cover important invertebrate species (e.g. of Odonata, Lepidoptera, Arachnida) in river corridor habitats; and to cover terrestrial habitats which are functionally similar to river corridors (e.g. hedgerows, farm headlands, railway embankments).
4. Research should be initiated into the detailed habitat requirements of riparian invertebrates, using indicator groups such as Coleoptera, Lepidoptera, Arachnida and Hymenoptera, to determine the 'functional habitats' of the riparian zone (a parallel to R&D 346 dealing with in-channel invertebrate functional habitats).
5. Research should be undertaken into the communities of plants of the river corridor, building upon the National Vegetation Classification, so that RCS plant species data can be accurately classified. The community categories will then indicate habitat conditions, defined by factors such as water table, pH etc. which cannot practically be considered in RCS.
6. The NRA should promote the development of full RCS as essential components of all Environmental Statements (ES) for all kinds of catchment development (particularly floodplain and channel). This would, in parallel with pollution assessment for ES, help to develop a philosophy of 'catchment conservation' among development agencies who might otherwise be very site-focussed.

1. INTRODUCTION

Management of water resources (land drainage, flood relief, amenity, fisheries, water supply and disposal) has been influenced by increasingly sophisticated statutory regulations. There has been a parallel development of the technology for water managers to meet cultural and environmental objectives, and of the scientific basis for such technology.

The creation of a national regulatory body has brought the opportunity for (and a need for) consistent methods in river evaluation, management and project appraisal. The current project aims to review and present information about the habitats of river corridor species, as part of a suite of environmental R&D investment which the NRA has initiated.

1.1 Statutory background

In the modern climate of agricultural and urban intensification, rivers are often the sites of greatest conservation interest, and their corridors provide a vital link between isolated pockets of natural habitat. The river network is therefore a nationally-important wildlife resource, which traverses conditions of geology and relief. Rivers are usually modified rather than destroyed by technological progress, in contrast to most other natural habitat types. Nevertheless, degradation of riparian and channel habitats can profoundly affect their natural communities, and sympathetic river management is a continuing priority for water managers. The legislature of England and Wales has laid an increasing requirement for conservation upon the water industry in all its forms.

In the late 1960s, water undertakings were expected to 'have regard to ... conserving natural beauty and amenity' during their manipulation of river corridors (1968 Countryside Act). Their only specific requirement was (where reasonable) to allow for public recreation along / in waterways. In the early 1970s, there followed a rationalization of the water industry whereby the numerous River Boards were replaced by ten regional Water Authorities (1973 Water Act). The Water Space Amenity Commission (WSAC) was set up to act in an advisory role, regarding national water policy. The members of this commission were:

- Central and local government.
- Water Authorities.
- Countryside Commission.
- English Tourist Board.
- Sports Council.
- Conservation and recreation organizations.

It was stated that 'in formulating or considering any proposals ... water authorities ... and the appropriate ministers ... shall have regard to the desirability of preserving natural beauty, of conserving flora, fauna and geological or physiographical features of special interest ... and of protecting ... objects of architectural, archaeological or historic interest' (1973 Water Act). The relevant Water Authority would be notified, should the NCC deem a proposed development site to be of special interest. However, the desirability of such features was simply to be heeded; there was no duty to actively preserve them; and land drainage functions took precedence.

Every Water Authority had a duty laid upon it to: report upon a regional survey of the management, uses and quality of water; estimate future water-demands over the next 20 years; and prepare a 20-year plan aimed to increase management efficiency, secure forecast water requirements and augment the 'wholesomeness' of waters. However, this duty did not address the issues of wildlife conservation, dealing solely with the practicalities of water supply, flood control and land drainage.

The 1974 Control of Pollution Act gave Water Authorities powers to remedy or forestall water pollution, by alteration or revocation of consented discharges. It also became an offence to alter flow regimes by removal of instream deposits or deposition of cut/uprooted vegetation in the channel, without the permission of the Authority (which was exempted in pursuance of land drainage or navigational duties). The 1975 Salmon and Freshwater Fisheries Act made it an offence to efflux pollutants (solid or liquid) into freshwater to the extent that the fish, their spawning grounds or their food supplies were harmed – although the efficacy of the statute was reduced on four counts:

- A definition of 'harm', against which to establish contravention, was absent.
- An acceptable defence was that the 'best possible means within reasonable cost' had been used to avoid the contravention.
- 'Traditional' effluxes (occurring since before 18-7-1823) were exempted.
- Effluxes sanctioned by an earlier statute were exempted.

Whilst undertaking their statutory duties, the Water Authorities were also exempted from the controls of the 1975 Conservation of Wild Creatures and Wild Plants Act which provided special protection for named species.

The 1976 Land Drainage Act consolidated previous legislation relating Water Authorities and their functions. MAFF were given the power to call for a public enquiry into any drainage plans which were felt to be contentious, though this power has rarely been exercised. The Water Authorities were enabled to produce bye-laws as deemed necessary to protect their drainage functions (regarding tree-planting, fence erection etc.). The general conservation aspects of the Authorities' projects were again overlooked, although they were required to pay 'due regard ... to the interests of fisheries'.

The 1981 Wildlife And Countryside Act provided a subtle, but important, change to the wording of the Water Act 1973 – a new duty was laid upon the Water Authorities to 'so exercise their functions ... as to further the conservation and enhancement of natural beauty and the conservation of flora, fauna ... where consistent with other duties'. In addition to this, the advisory role of the NCC (regarding sites of special interest) was increased: the Water Authorities were now expected to consult with the NCC prior to any works on notified sites (except for emergency operations).

The water industry was again re-organized when the 1989 Water Act divided the functions of the 10 Water Authorities into 2 sectors:

- Water companies (PLCs); providing water supply and recovery.
- National Rivers Authority (NRA); with diverse responsibilities, including regulation of the PLCs.

The NRA is a non-departmental public body with a staff of 6500 across ten regions, corresponding with the ten previous Water Authorities. Its operations fall into seven functions, which are: water quality; water resources; flood defences; freshwater fisheries; conservation; recreation; and navigation.

1.2 Scientific background

Habitats are built up by the interaction of natural (e.g. geomorphic) and human (e.g. landscape) forces. They have a central role in the ecosystem, providing the basis for richness of species and communities. The concept of habitat is not new, nor is it unique to river systems; it was important in early ecological thinking (Elton 1966) and has developed ever since (Bell, McCoy & Mushinsky 1990). River Corridor Survey methodology – developed from the Nature

Conservancy Council's original methodology, through Holmes' (1986) review of examples to present-day practice (NRA 1991) – has followed a modular, habitat-based approach which is the most flexible and practicable (Fig 1.1).

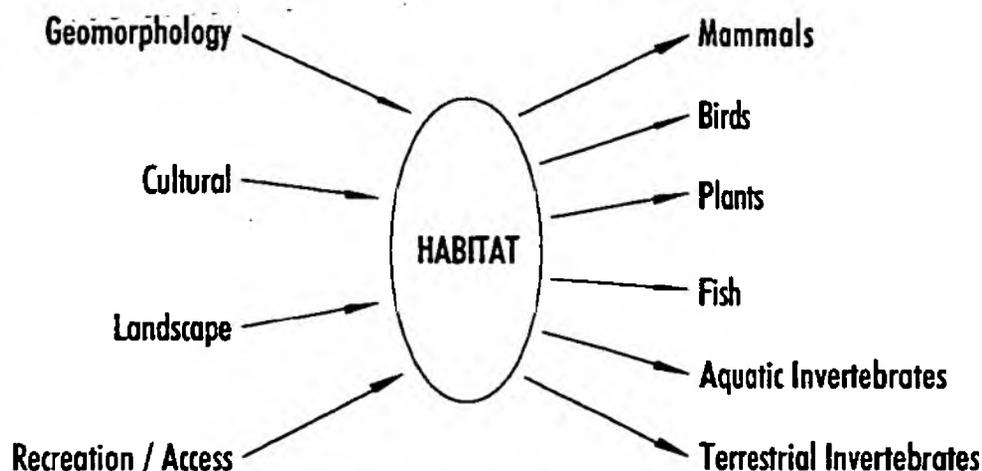


Figure 1.1 The basis for habitat-orientated River Corridor Surveys (after NRA 1991)

River Corridor Surveys have focussed upon both habitats and species in practice, albeit usually species of flowering plants and birds (Coles *et al.* 1990). The identification of species can follow fixed rules; it is supported by keys; and can readily indicate value categories based on conservation criteria such as rarity. No such clear written guidance exists for habitat identification, except for the original basis of the methodology, Ratcliffe's (1977) review and more recently, the handbook compiled by Lewis and Williams (1984). This report reviews the available literature to provide an objective reference for habitat identification where it exists.

'Habitat' is ecologically a rather vague term, since in the extreme any patch of the environment is a habitat to some organism or other. In the practical context of River Corridor Surveys, it is necessary to narrow the concept to that of a 'functional' habitat. These have been defined as habitats which can be reproducibly identified, and which are known to support assemblages of species distinct from one another. For NRA purposes, we should probably add habitats which are known as requirements for individual species of high conservation profile or amenity value.

The concept of a functional habitat for species assemblages was first introduced to the NRA in the context of river invertebrate communities (Smith *et al.* 1990a, 1991, Harper *et al.* 1992). It is broadly similar to the concept of community classification on a larger geographic scale, such as the National Vegetation Classification of the British Isles (Rodwell 1991), but defines the habitat in terms of visual attributes rather than species assemblages.

Some attempts to describe a functional habitat for individual species have also been made, primarily for fish species (Bovee 1978, 1982). These take a different approach, initially finding the species' occupation of conditions defined by physical variables (e.g. depth, velocity, substrate). Habitat use is then considered with measurements or predictions of the abundance of habitat combinations in the stream, to calculate overall suitability of the stream for the species. The method has been most successful in modelling the effects of water quantity on habitat.

A complementary approach is to build up a review of the habitat requirements of individual species, and then prepare a composite picture of habitats from these. Inevitably this

is a selective process, as few out of the total number of riparian and channel species have been studied. Larger species are generally more likely to have been studied in enough detail for habitat requirements to be known. Larger species are also more mobile, so their habitat requirements are separated more in space and in time. This makes a functional habitat approach more difficult unless it is possible to define a functional habitat based upon the proportions of time spent in it, such as the IFIM method applied for fish (e.g. Kershner and Snider 1991).

1.3 Outputs

The output from this project is two-fold:

1. Field handbook: a concise habitat-based guide for use on site by surveyors.
2. Species / habitat review: a more comprehensive text for desk-top use.

The field handbook aims to list the species (or species groups) generally associated with defined habitat features which might be recorded in the river corridor or channel. It is hoped that this will act as a reference aid to enable the river corridor surveyor to more accurately note important features or their associations. The handbook has been submitted as a separate volume, and as part of the R&D Report.

The species/habitat review in this Project Report can be used to expand upon the bare facts presented in the handbook, or to aid investigation into particular interests. The contents of this volume are the results of an extensive literature review conducted throughout the project. Citations in the text should provide a good reflection of the available literature – to be used as they stand, or as the starting-point for further searches.

A habitat-orientated review has been carried out for several components of the riverine system, forming chapters 2 and 3 of this report. The approach was particularly applicable to terrestrial vegetation, because of developments in the field of phytosociology; and to stream invertebrates, because of continuing research by the NRA, IFE, JNCC and corresponding bodies in a range of other countries.

The species-orientated approach was most favoured, and thought most feasible, by conservation staff within the NRA regions during the initial liaison phase of this project. A working list of important species to be reviewed was then drawn up as a result of this consultation. The species reviewed in the time available are mainly birds and mammals, with some amphibians and fish. This approach forms chapters 4-7 of the report. Each section is preceded by a basic distribution map and a habitat summary listing the broad habitat requirements of the species. The summaries do not aim to replace the complete sections, only to prompt the reader regarding general relevance, and as such some of the associated categories might appear unnecessarily broad.

2. RIPARIAN AND FLOODPLAIN HABITATS

Physical conditions – the nature of soil and water – primarily provide functional habitats for plant communities, and then physical plus vegetational habitats provide for animal communities.

2.1 Plant communities

2.1.1 Introduction

In the floodplain and riparian zone, much evidence for habitat distinctiveness comes from terrestrial as well as aquatic studies, but particularly from the detailed analysis of vegetation types known as phytosociology (Rieley and Page 1990).

The most dominant physical feature in the floodplain influencing plant communities is water table depth; and superimposed upon this is soil material. This combination leads to conditions of water chemistry (e.g. pH, nutrient availability and oxygen tension) which exert more subtle influences upon the composition of the plant community. Visible aspects of this – types of standing waters or waterlogged ground – are already recorded under the RCS adoption of the NCC Phase 1 survey methodology. Chemical aspects are not covered, though simple measurements of standing water could be made, such as conductivity and pH. Many plants are pH-indicators (e.g. *Sphagnum* species: Rieley and Page 1990) but the invertebrate communities of waterbodies in the floodplain are often more strongly influenced by pH than are the plants (e.g. Friday 1987).

2.1.2 Riparian

River corridor surveys in their current form superimpose the recording of vascular plants upon the NCC habitat survey methodology, and the data are additionally interpreted in terms of species rarity value (e.g. Brooker 1982, Slater *et al.* 1987, Coles *et al.* 1990). Correlations have been shown between species richness and habitat richness, such as the 'habitat features' list of Welsh river surveys (Brooker 1982, Slater *et al.* 1987), but there is little documentation of direct habitat analysis. Morin *et al.* (1989) analysed the bankside flora of rivers in Montreal, showing that multivariate analysis of the species recorded (156 spp.) and of abiotic habitat variables (e.g. pH, soil particle composition, nutrient content, ground slope, light, drainage) gave a similar classifications.

Elsewhere, identification of functional habitats for plants has been carried out largely through the detailed analysis of plant communities themselves. This approach, phytosociology, was pioneered for vegetation analysis in Europe at the beginning of the century by Braun-Blanquet and others. It was initially qualitative and subjective, but has developed into a sophisticated and detailed classification of vegetation types (Ellenberg 1988). It is based upon the multivariate analysis (e.g. indicator species analysis) of plant species' abundances, interpreted using information from decades of autoecological research. The assemblage of species at any one place, compared with the classification system, thus provides the most detailed available information about the habitat mosaic of the wetland/riparian communities.

Phytosociology defines plant associations entirely by floristic composition; but because of the detail of the classification these associations (within alliances) represent the occupation of definite habitats. The classification system is hierarchical, in a similar fashion to a taxonomic classification, with a class as the coarsest grouping, followed by order, alliance and sub-alliance. There are eight main groups with up to eight classes in each (e.g. eight in the

freshwater and mire group, seven in the disturbed herbaceous group), and 2-3 orders in each class. River corridor surveys may thus select the level of detail required for a particular purpose.

There are five steps involved in the identification and characterisation of associations:

1. Field description.
2. Tabular organization of data to represent local variations in vegetation.
3. Checking ecological reality of units extracted in the field.
4. Investigation of similar patterns in other localities.
5. The erection, differentiation and characterisation of associations.

Steps 2-5 are usually computer-based. Field descriptions include records of plant species in representative quadrats, with a quantitative estimate of three features; cover-abundance, sociability (e.g. single, patchy, mat) and constancy (regularity of appearance in quadrats).

Publication of the British National Vegetation Classification (NVC) will be completed in five volumes by the end of 1993, with the first two already published (Rodwell and Pigott 1991a,b). The total number of plant communities recognised as distinct is around 300 (Rodwell 1991). This will provide a powerful stimulus to habitat and vegetation classification generally and the plant habitat objectives and methodology of RCS should probably be reviewed at that time. The analytical methodology of the NVC is now reproducible on desk-top PCs, so that it will soon be possible to produce a classification of vegetation communities matching the NVC.

Most undertakers of RCS do not have the resources of time or manpower to follow the quadrat-based fieldwork of the NVC, instead recording species lists in defined areas or river bank sections (usually 500 m). It is still possible to analyse presence/absence data over a set of such sites and this has been done on riparian woody plant species (Mason *et al.* 1984, Mason & Macdonald 1990). In both mid-Wales and eastern England they found a woodland tree association, corresponding – but different in indicator species – to the broadleaved woodland association Alno-Ulmion (8.433) of Ellenberg (1988), together with a shrub and hedgerow community similar to association Rubo-Prunion (8.411). In East Anglia they also found two assemblages of lowland floodplain woods, corresponding to association Salicion albae (8.112); and in Wales a heathland shrub community and an ornamental community without clear analogues in Ellenberg's scheme. In a detailed study of the Great Ouse catchment, Kemp-McCarthy (NRA R&D 526) has classified both woody and herbaceous vegetation using TWINSPAN and occurrence data in 500 m bank lengths. Woodland assemblages in addition to the above included elm and poplar (plantation). There was also a mosaic of stream reed bed, mud bank, waste ground, arable weed, grassland and wet meadow communities.

Other linear habitats which bear some similarity to riparian corridors are railway lines. The vegetation of these was the subject of an intensive investigation in the late 1970s (Sargent 1984). The types of disturbance and management and their effects on vegetation are unique, but there is enough similarity for comparisons to be drawn. Sargent, covering the whole of Britain, found 32 subcommunities, including analogues of the vegetation types described above.

An expert system for matching field data with the NVC and the European (CORINE) vegetation community types is under development, recognizing that ecologists using the NVC may not have the time to sample plant quadrats. The system, TABLEFIT (Hill 1989, ITE 1991) may well enable RCS plant species lists, particularly if they are in rank abundance, to be matched to the nearest equivalent vegetation type.

The National Vegetation Classification is not very precise in its dealings with managed edge environments such as riverbanks, so a valuable NRA development would be a detailed investigation of the phytosociology of riparian vegetation, leading to a working classification

for future RCS use. In the meantime RCS species lists could be classified and/or matched to the NVC (Rodwell and Pigott 1991a,b) to provide a catalogue of community types.

An alternative approach might be to allocate each plant species a score based upon its tolerance of water table depth and then to simply summarise the scores for all species in a sample (e.g. mean or modal score). Ellenberg (1988) allocated scores from 1-12 (extreme dryness - fully submerged) for each of around 2000 European plant species as part of a wider ecological indicator classification. It is feasible, at least for wetland vegetation if not riverbank, to obtain an indication of the habitat mosaic by analysing the plants in this way, particularly using a computer programme. Similar indicator values for light, pH and nitrogen exist and the combination of the four could produce a habitat classification if the species records come from small enough units (certainly sub-divisions of the 500 m river stretch would be needed).

2.1.3 Lotic

The phytosociological approach to vegetation classification covers all forms of plant communities, from those of torrential flow to damp meadows and woodlands, but is primarily based upon vascular plants and bryophytes in or on soils. It also relies heavily on data from quadrats, which are difficult to execute in open water. In upland and torrential rivers and streams, bryophytes and algae are more dominant members of the plant communities, and the habitat mosaic of these plants may not be accurately reflected by the classification. Despite this methodological difficulty, several detailed studies of British aquatic plant communities have been carried out, either using presence/absence in transects, measured river lengths or additionally incorporating some abundance estimate. These studies, which have included bryophytes and algae, have mainly been carried out by Haslam (Haslam 1978, Haslam and Wolseley 1981) and Holmes (e.g. 1984). Haslam's studies provided considerable knowledge about the habitat requirements of individual species in rivers, which was built upon by Holmes in a hierarchical classification of 56 river types based upon TWINSPAN analysis of their channel and bankside flora. Ormerod *et al.* (1987) performed a similar, though less extensive, analysis of aquatic flora in Welsh upland streams, revealing four vegetation groupings related to pH rather than any measured habitat features.

These studies all illustrate the problem of obtaining clear habitat information from community analysis of aquatic species, particularly fully aquatic ones. Between sites, most of the variation can be explained by water depth and water chemistry. Habitat is probably of equal importance in determining plant communities at a site but systematic information is rare. The depth, flow and substrate mosaic of the river channel should be recorded as an annotated map for each stretch in the RCS since this set of habitat conditions is also important for invertebrates and fish. The water chemistry indicators pH and conductivity should be recorded if not available from water quality records; these parameters together will indicate the habitats available for plant communities based upon Holmes' classifications.

2.1.4 Lentic

Standing water bodies range in size through lakes and reservoirs; disused quarries and pits; ox-bows and farm ponds; to temporary flood waters in floodplain depressions. Drainage ditches (essentially lentic) are also important. This mosaic of standing water types provide habitats for a range of plant communities which might not be fully developed in the quieter reaches of the stream channel, because of flood events or channelization. Standing waters also provide a refuge from main channel pollution or eutrophication, as in the Norfolk Broadland (George 1992). The vegetation communities of standing water have been described by phytosociology, so any interpretation of RCS species records can proceed in the same way as outlined in Section 2.1.3, provided they are kept separate for each distinct water body.

Spence (1964) classified 49 community types: depth, light, water chemistry (indicated by pH and conductivity) and degree of permanence (measured as depth in summer) are the main controlling factors which should be recorded in RCS. Plant zonation is often most obvious in the littoral zones of water bodies because of depth and substrate zonation. Other features which contribute to plant species richness, particularly in recently-constructed ponds, are presence of a berm and the amount of throughflow (Bowen 1991). If plant species cannot be recorded because of time limitation, then a rapid surrogate would be plant growth types - emergent, marginal, floating-leaved, submerged - as an indication of habitat diversity.

Several studies have been undertaken to try to identify the important factors determining plant community structure in ponds, by multivariate analysis of a range of environmental variables recorded from a large number of ponds. Often these studies have included a parallel invertebrate community analysis (e.g. Friday 1987). Generally the association of plant species with environmental factors has been less easy to establish than that of invertebrate species, probably because of the importance of initial reservoirs of colonists. Until clear relationships are known, depth, morphometry, substrate type, permanence, origin, degree of shading and pH/conductivity should be recorded for all water bodies which fall within the RCS. Methods for analysis of the data should be made to allow for missing data due to problems such as turbidity.

2.2 Animal communities

2.2.1 Woody vegetation

Riparian woody plants provide food and shelter. Food provision extends spatially, through leaf fall and invertebrate movements; and temporally, through the breakdown of leaf litter. Leaf litter is a particularly important allochthonous input to the energy budget of streams.

Southwood (1961) and Elton (1966) compared the invertebrate communities of trees, finding that many invertebrates were restricted to particular tree species. Some trees (e.g. oak) have a particularly high number of associated invertebrates. Southwood explained that this is a result of the cumulative abundance of a particular tree type throughout recent history; a species that has been present in Britain during the majority of the Quaternary period has had a greater potential for encounter and adaptation of prospective grazers.

There is little evidence to suggest that invertebrate species richness is affected by the number of trees of the same species in any one place, although there is a clear correlation between the richness of the fauna and the overall abundance of the species in Britain (Southwood *et al.* 1987). It is likely though, that fewer species will occur on solitary trees because a woodland changes the microclimate and physical environment (e.g. Geiger 1950) which will increase the number of habitats available to animals. Information about the development of invertebrate fauna with age and size of the tree is lacking, but it may be assumed that an older tree supports an increased fauna as additional habitats are added - rot holes, bark sculpture, aerial dead wood, epiphytes (Barkman 1958). An alternative increase in habitat richness of individual trees is provided by pollarding. This practice expands the crown of the tree (usually willow) into a platform or depression up to a metre or so across, which may be colonised by debris, plant seeds, fungi and animals. Over 100 epiphyte species have been recorded from pollarded riverine willows (e.g. Thompson 1925) which gives an indication of the possible number of invertebrates, though no study could be found which compared invertebrate richness in pollared and non-pollared trees.

Infall to the stream channel from riparian trees has three main forms: leaf litter and woody debris (see Section 2.2.3); fall of terrestrial invertebrates; and secretions or faeces of herbivores

such as aphids. Input of terrestrial invertebrates is highest in the spring and summer, coinciding with their emergence as adults (Mason and Macdonald 1982). Mason and Macdonald found that sycamore yielded the greatest numbers and biomass of fallen invertebrates, followed by oak, alder and ash (Table 2.1). Sycamore trees are also host to large populations of aphids which provide honeydew, a secretion rich in sugars and nitrogen. The collection from beneath the ash canopy did not differ significantly from that collected at an open control site. Southwood (1961) identified 284 insect species from oak, 90 from alder, 41 from ash and 15 from sycamore. The value of trees to invertebrate species richness and biomass therefore contrasts, such that diversity is an important attribute of the canopy for conservation.

Table 2.1 Biomass of invertebrate fall on the River Arrow (Mason and Macdonald 1982)

Taxon	g m ⁻² dry weight (mean of 4 collections over a 28-week period)				
	Control	Ash	Alder	Oak	Sycamore
Arachnida	1.50	1.07	1.75	1.94	1.66
Isopoda		0.01	0.10	0.32	0.64
Collembola	0.01	0.01	0.03	0.01	0.04
Ephemeroptera	0.03	0.10	0.08	0.02	0.01
Plecoptera	0.08	0.18	0.20	0.17	0.10
Orthoptera			0.18		
Dermoptera		0.12	0.18	0.23	0.71
Hemiptera (Homoptera)	0.89	0.72	1.42	1.53	4.29
Hemiptera (Heteroptera)	0.17	0.33	0.55	1.17	2.04
Hymenoptera	0.81	0.18	1.02	0.78	0.86
Coleoptera	2.66	2.36	2.27	2.55	3.93
Megaloptera	0.04	0.17	0.10	0.32	0.40
Neuroptera			0.01	0.02	
Trichoptera	0.61	1.87	1.09	0.79	2.75
Lepidoptera (larvae)	0.18	1.44	1.51	9.95	2.18
Lepidoptera (adults)	0.27	0.23	1.71	0.59	3.13
Diptera	2.60	2.28	8.09	7.31	12.94
Thysanoptera	0.07	0.08	0.11	0.08	0.12
Total	9.92	11.15	20.39	27.76	35.80

Trees provide a habitat for birds as physical structures (for roosting, nesting) and as a direct (seeds, berries) or indirect (invertebrates) food source (MacArthur 1964). The species richness of woodland birds depends considerably upon habitat unit size (Helliwell 1976, Hinsley and Bellamy 1991), with woodlands below 2 ha containing fewer species in less stable populations, and more field and edge species. RCS records should include the species of trees together with notes on estimated age (or height as a surrogate), physical structure and attributes such as holes, dead branches, and distance from the stream channel. Any aggregation of trees should be noted with estimates of area and of shape (e.g. ratio of area/circumference).

In the river corridor, continuous stands of mature trees are infrequent unless the river flows through a woodland or the trees have been planted. More often the woody community is dominated by shrubs and the character of the riparian zone is hedgerow-like. Shrub species generally differ from tree species in that they are insect (rather than wind) pollinated and their fruits are dispersed by animals, particularly birds. Elton (1966) reviewed the fauna of hawthorn and wayfaring tree (*Viburnum opulus*) in particular, both as examples of shrub species and in the context of a hedgerow community. He concluded that the invertebrate community – nearly all less than 5 mm – was composed of species relying upon the leaves, flowers and epiphytes. The main period of invertebrate abundance was April-August, with a succession of dominant groups. Predatory invertebrates were widely distributed between various habitats and were

polyphagous. There was a range of selectivity, with some invertebrates confined to one of the plant species, and generally two distinct communities. For invertebrates it seems that each shrub species should be considered a different functional habitat.

A distinct category of 'shrub' is provided by ivy (*Hedera helix*), which grows usually as an epiphyte on trees. Ivy is of habitat importance in its own right, for two reasons. Its flowering and fruiting seasons are asynchronous with other shrubs (flowers in autumn, fruits in spring) – so flowers provide an essential nectar source for late-flying insect species whilst fruits are winter food for both invertebrates and vertebrates (Elton 1966). Its growth form, a dense climber of tree-trunks and walls, provides good nesting sites for small birds.

Bird species also utilise shrub and hedgerow-type habitat and some are dependent upon it, such as fieldfares and redwings which feed on berries in the winter. The number of bird species generally depends upon the height of the shrub layer (e.g. Pollard *et al.* 1974). Continuous areas of low-growing shrubs such as blackthorn or bramble are valuable for the provision of dense areas of food and cover for small birds; but are often considered as indicators of neglect by river engineers. RCS records should include species composition of the shrub community and both its horizontal and vertical structure.

There is a growing body of work which has analysed the corridor value of linear habitats such as hedgerows as shelter belts for mammals and birds. Bennett (1990) found that riparian and roadside corridors were essential for the maintenance of small mammal populations in remnant woodlands. The woodlands on their own could not support an adequate population size but corridors provided opportunity for dispersal and gene flow. Such work shows the overall value of linear semi-natural vegetation corridors; but does not indicate the importance of individual habitat features or conditions. In particular, the required habitat dimensions for vertebrate corridor effectiveness are not well known and the majority of research has been in Europe (mostly The Netherlands), USA and Australia.

2.2.2 Herbaceous vegetation

River corridors most frequently consist of wetland, meadow or disturbed ground associations of herbaceous plants. They form a thin strip between the river and adjacent land use (usually agricultural). In this sense they are similar to roadside verges, railway lines and field headlands, all of which have been studied recently. Elton (1966) suggested that herbaceous vegetation structure is more important than its species composition to many invertebrates such as grasshoppers, stem-boring Diptera and spiders. More recently, several studies have focussed upon the role of plant 'architecture' on spiders (Duffey 1966, Robinson 1981, Gibson *et al.* 1992) and upon the use of various taxa of invertebrates as ecological indicators (Clausen 1986, Sterling *et al.* 1992). Four vertical zones up to about 60 cm – termed ground, turf, short grass and long grass – are utilised by different invertebrate species. Some species also require the dead stems of tall herbs such as cow parsley for overwinter survival; and the taller habitats support an accumulation of litter which increases species richness through support of detritivores. Tussock-forming grasses are important for insect overwintering and as a physical component for birds (Trewick *et al.* 1991). RCS records should include an estimate of the proportions of the four 'zones' in riparian grassland, together with an estimate of grazing pressure (Gibson *et al.* 1992).

Watertable depth in riparian grasslands is of major importance in controlling the availability of invertebrates to birds. These include waders which feed by probing (beak penetrates damp soil more easily) and those feeding on drowned invertebrates and the early aquatic colonists (e.g. Hemiptera, Coleoptera) of temporary pools. Wetness inevitably varies throughout the year; but should be recorded wherever possible in RCS for wet grasslands, from available signs such as vegetation changes, topography and debris strand lines.

Management affects the value of grassland to both invertebrates and birds. Grazing has a variety of effects. Light grazing suppresses wetland grasses such as *Glyceria maxima* which are less palatable to herbivorous waterfowl; and provides invertebrate habitat in dung pats and trampled surfaces. Heavy grazing causes poaching and an increased risk to ground-nesting birds. Mechanical cutting may simulate low-intensity grazing to the benefit of herb species richness, with damage risks related to timing of the cut. An outline review of the major management issues is contained in Treweek *et al.* (1991). Notes on the grazing intensity (stock species and density estimate) or cutting regime of grassland would be useful, but difficult to include consistently in RCS.

The plant species richness of some herbaceous communities has been shown to affect invertebrate richness. Saville (1991) has shown a correlation of bumblebee numbers with the number of flowering plant species, particularly species of high nectar provision, in open or edge habitats of farmland. She found that habitats providing the best forage for bumblebees were unmown ditches along field boundaries and areas free from evidence of recent herbicide application. Phytophagous invertebrates have now been extensively studied (Ward 1988). The insects associated with umbellifers are a mixture of specialized and generalist feeders (Jones & Lawton 1991); and this seems to be the case for other plants (Strong *et al.* 1984).

Other nectar feeding insects such as Lepidoptera probably have a similar abundance relationship with flowering plant species; and they often have a more or less specific larval dependence on food plants. The food plants of the 58 species of British butterflies are relatively well known although there is far less information about those of the c. 2500 moth species. Butterfly colonies may often be maintained on small areas of linear vegetation such as woodland rides where food plants occur together with sunny shelter of shrubs (Thomas and Lewington 1991) so it is likely that river corridors form suitable habitat. The combination of shrub edge and grassland could be noted on RCS sketch maps and many butterflies are identifiable in flight. Major food plants could be flagged from the vegetation species lists, on which important types include:

- Grasses: *Agrostis*, *Festuca*, *Poa*, *Dactylis*, *Phleum*, *Brachypodium*, *Holcus*.
- Herbs: *Succisa*, *Urtica*, *Cirsium*, *Lotus*, *Helianthemum*, *Rumex*, *Cardamine*.
- Climbers: *Lonicera*, *Hedera*.
- Shrubs: *Ulmus*, *Salix*, *Prunus*, *Rhamnus*, *Frangula*, *Euonymus*.

2.2.3 Litter and woody debris

The litter layer is an essential element of nutrient cycling and a habitat for numerous decomposer and detritivore species, especially in woodland (Packham and Harding 1982) but also in vegetated river corridors. Pieces of dead wood were shown by Elton (1966) to provide habitats for various communities of detritivores and their predators, according to size and location. Dead wood on trees differed from that on the ground; and habitat complexity was further augmented by bracket fungi. In the Wytham wood area of Oxfordshire, 18 species of birds (e.g. little owl, woodpeckers and tits) depended upon standing dead wood for nest sites.

Waterborne and stranded woody debris has been shown as an important habitat component of the river corridor, and possibly an important mechanism for invertebrate dispersal. Over 300 species of beetles were recorded in flood debris on the River Cherwell and River Mole (Walker 1908, Easton 1947) and it is an important feature in the survival of riparian beetles during spates (Anderson 1968). The streambank retention of such debris, which frequently persists throughout the year, depends upon overhanging branches of trees (e.g. willow and alder) and stems of shrubs. Coarse woody debris – and the apparent cause of its retention – could be recorded in RCS.

2.2.4 Marginal / emergent vegetation

Terrestrial invertebrates utilise the aerial parts of marginal and emergent vegetation in much the same way as they do herbaceous riparian vegetation. In many cases, the mature stages of otherwise aquatic invertebrates also use this vegetation zone for feeding, mating and oviposition. Some emergent species provide habitats in their own right: *Phragmites australis* hosts a unique faunal and floral community (Durska 1957, Skuhrávy 1978); and the specific fauna of *Cyperus papyrus* (not British) changes with the stage of development of the umbel (Thornton 1957).

Studies of the marginal emergent vegetation of Czechoslovakian fish ponds have shown distinct faunal changes corresponding with vegetation changes (*Glyceria*, *Sparganium*, *Carex*) in the transition to dry land (Dvorák 1978). This kind of evidence suggests that the identification of distinct vegetation communities will itself take into consideration the distinctness of invertebrate communities. Murdoch (1963) has shown that the carabid beetles inhabiting marshy areas divide into two species groups: those inhabiting vegetated areas which leave a litter layer overwinter (the plant species seems unimportant); and those inhabiting open ground.

Much information about the role of marginal and emergent vegetation as invertebrate habitat is vague. The feeding, territoriality, mating and oviposition of many dragonflies depends upon this vegetation (Hammond 1983) but usually is not species-specific: detailed studies of the habitat use of ovipositing *Leucorrhina intacta* recorded 'shallow water over submerged vegetation' and 'emergent vegetation' as preferred sites for oviposition (Wolf and Waltz 1988). Erman (1983) came to similar conclusions about other aquatic insects at different stages of their life cycle – the habitat requirements are for shallow edges and variety in plant structure. The larvae of aquatic species sometimes, as an exception, had more precise nocturnal feeding requirements.

2.2.5 Bare substrata

Several studies have shown that bare substrata, stripped by winter floods and colonized only by pioneer plant communities, have distinct invertebrate assemblages.

Plachter (1988) found 48 carabid species in four distinct riverine habitats in Germany:

- Wet, plant-free shore areas of gravel bars near to the water's edge.
- Dryer, but also plant-free centre of the bars, farther away from the edge.
- Isolated stands of vegetation surrounded by gravel.
- Fine sand or sand-clay slopes at the outer edge of bars covered with grasses and less frequently inundated.

Fowles (1990) found habitat partitioning of carabid species with particle size on shingle banks in Wales and reviewed similar works elsewhere in Britain. The importance of the habitat mosaic of shingle banks is not confined to beetles: evidence also exists regarding wandering spiders (Uetz 1977) and ladybirds (Majerus and Fowles 1989), many species of which seem to be national rarities. Some may be on the edge of their range and confined to this one habitat because it is ephemeral and hazardous, so reducing competition. Whitaker *et al.* (1979) discussed the nature of the flood hazard for a chrysomelid beetle, their study stressing the importance of adjacent populations for re-colonization.

Anderson (1969, 1983, 1989) working in Norway, classified carabid riparian habitats in more detail, in terms of particle size (including vertical heterogeneity such as stones on silt, cobbles on sand), degree of moisture and plant influence. About twenty microhabitats were

separated according to preferences within the tribe Bembidiini, and defined by combinations of the following:

- Substrate at surface (cobbles, stones, gravel, sand, silt)
- Substrate below surface (sand, silt)
- Elevation (low lying, intermediate, never flooded); hence moisture content.
- Vegetation cover (grasses and herbs, shrubs)
- Degree of shading (open, part shade, dense shade)
- Presence of woody debris or leaf litter.

A wider riparian habitat classification was developed by Lott (1992) from a preliminary study of terrestrial beetles (mostly Carabidae and Staphylinidae) in the floodplain of the River Soar. There was some overlap in species composition between all sites, but four main habitat types were:

- 'Pioneer' sand and shingle banks disturbed by floods.
- More stable sand and silt bars.
- Undisturbed meander cutoffs with a well-developed litter layer.
- Permanently waterlogged sites.

At least the first three habitats represent stages in a temporal succession, as well as being spatially distinct.

Some indication exists in the literature that more vertical bare sites have their faunal importance. A survey of bees in Cheshire (Whitfield and Cameron 1988) suggested that species richness along the River Dean (26 solitary species, 9 social and parasitic species) was related to the suitability of bank soil for nesting; and to several nectar sources such as riparian shrubs.

Anderson's (1969 *et seq.*) habitat classification is the most detailed of those described above, and can incorporate within it the categories from other studies. Each of Anderson's Norwegian habitat components could be recorded for riparian depositional substrates, although we do not at present have such detailed information on their importance to UK fauna.

2.2.6 Lentic

The aquatic invertebrate communities of several different sets of standing water bodies have been studied and classified. Friday (1987) worked on 16 clay ponds in Dorset; Bowen (1991) on a range of newly-created water bodies in the River Wissey catchment; Luff *et al.* (1991) on 302 standing water sites in the River Tyne catchment; Pond Action (1991) on 111 ponds across Britain; and Verdonschot (1992b) on 157 ponds in The Netherlands.

The parameters of importance which define the community types in these studies are the same as those which have been reviewed for plant communities above, with the addition of the nature of the aquatic vegetation. Verdonschot (1992b) produced a classification of nine pond types, described thus:

- Temporary, acid, mesotrophic.
- Permanent, acid, mesotrophic.
- Acid, mesotrophic, slight organic enrichment.
- Small, shallow or swampy, acid-neutral.
- Small, shallow, acid-neutral, eutrophic, vegetation-rich.
- Clear, oxygenated, vegetation-rich.
- Clear, deep, oxygenated, vegetation-rich.

- Densely vegetated, organic enrichment.
- Large, organic enrichment.

Luff *et al.* (1991) distinguished fifteen standing water types from an analysis of water beetle assemblages:

- Open lakes and ponds, bare stony substratum, basic water.
- Open, large ponds, clay/sand substratum, basic water, well-vegetated edges.
- Open, large, clay ponds, poorly-vegetated edges.
- Large, permanent ponds, clay substratum, well-vegetated, little open water.
- Medium-sized, well-vegetated, clay-based marshes.
- Medium-sized, well-vegetated, temporary ponds.
- Small, well-vegetated, temporary pools.
- Small, well-vegetated, very temporary ponds.
- Small, well-vegetated, flushes or spring-fed pools.
- Well-vegetated, clay-based, stream-fed pools.
- Open, acidic lakes, clay-based, little vegetation.
- Acidic, shallow pools, some shaded and spring-fed.
- Acidic mires with slow-moving water.
- Upland acidic mires with static water.

Sites can be related to both of these classifications from estimates of size, degree of permanence, depth and extent of vegetative colonisation; together with measures of pH and conductivity (for trophic status); and perhaps a subjective estimate of degree of organic enrichment. Other studies have stressed the importance of open water over different substrata (e.g. for corixid species richness: Macan 1962, 1977) and adjacent vegetation for terrestrial stages of insect life histories (e.g. dragonfly territoriality: Clemick *et al.* 1980). Combining these parameters with those discussed for vegetation (Section 2.1.4), an effective habitat recording system for floodplain water bodies would incorporate at least:

1. Permanence: permanent, semi-permanent (never dry), seasonal (dry in summer)
2. Size: small (field pond size), medium, large (gravel pit size)
3. Shoreline / area ratio.
4. Depth: maximum, proportion less than 1 m deep.
5. Slope of littoral zone.
6. Substratum proportions of littoral zone.
7. Proportion of open water: total, and over different substrate types.
8. Proportion of vegetation types: riparian, emergent, marginal, floating, floating-leaved, submerged.
9. Plant species (or at least dominant ones in each vegetation type)
10. Shading: extent and intensity.
11. Adjacent vegetation, particularly proximity of woody vegetation.
12. Source of input water.
13. Elevation above sea level.

Waterbody characteristics have also been assessed for their suitability to birds (e.g. Thomas 1976, 1982; and reviewed by Treweek *et al.* 1991). Characteristics relevant to their preferred habitats are included in the listing above.

3. INSTREAM HABITATS

3.1 Fish

Over the past few decades several systems of fish habitat assessment have been developed – initially in the USA – based upon the measurement and prediction of hydraulic variables. This has become necessary because many aspects of river management (e.g. flow regulation, channelization, bank protection, habitat improvement techniques) affect river hydraulics; and consequently aquatic communities. Fish habitat evaluation studies have been used for various applications:

- Classification of existing conservation or fisheries value.
- Impact assessment of management proposals.
- Assessment of reach suitability for fish stocking.
- Comparison of alternative strategies for habitat restoration.

Towards several criteria:

- Fishes of sport or commercial value (and their competitors)
- Indicator species (i.e. those with narrow habitat tolerances)
- Rare and endangered species.
- Forage species (occupying an intermediate position in the food chain)

3.1.1 Instream Flow Incremental Methodology

The main technique developed in the 1970s, the Instream Flow Incremental Methodology (IFIM) predicts the amount of potential habitat under different combinations of flow regime, channel dimensions and slope for a given species or life-stage of a species (Bovee, 1978, 1982). Its objective is to provide a computer simulation of the stream length at different discharges, built up from a multiple of 'cells' based upon field data initially collected from a series of transects.

The main parameters recorded are depth, velocity, substratum and available cover. A computer programme determines a composite probability of use for each combination of parameters. It then calculates the 'weighted usable area', which represents the habitats' value for the species under study. The following steps are involved:

Stream reach simulation

The basis of the simulation is the prediction of hydraulic parameters (e.g. depth, velocity, width) for different discharges. There are several calculations available (one widely used simulation is called PHABSIM), of which most are based upon Mannings' equation:

$$Q = n^{-1} S^{1/2} R^{2/3} A$$

where Q = discharge (m^3s^{-1})
S = energy gradient
R = hydraulic radius: c-s area / wetted perimeter (m)
A = cross-sectional area (m^2)
n = roughness coefficient (obtained from tables and a subjective categorization of the stream channel)

The relationship can be manipulated for expression of various parameters, such as velocity:

$$Q = V A \dots \text{ where } V = \text{mean velocity (ms}^{-1}\text{)} \dots \text{ and hence } V = n^{-1} S^{1/2} R^{2/3}$$

Determination of variables within simulated reach

IFIM reach simulation uses several transects across the channel; each transect is then subdivided into 9-20 cells, each of which is basically treated as a separate channel (Figure 3.1). For each cell:

1. Mean depth and velocity are calculated.
2. Cell area is calculated by multiplying its width by [1/2 of the distance to the upstream transect + 1/2 of the distance to the downstream transect]

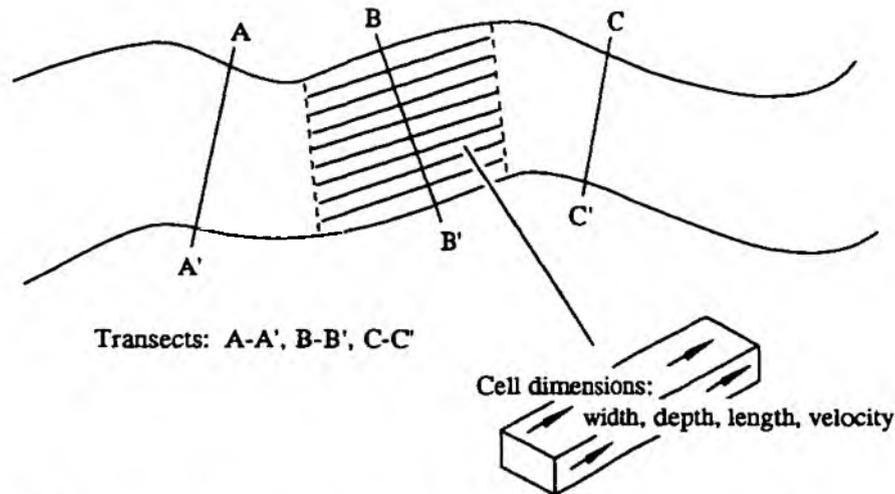


Figure 3.1 Stream reach simulation, modified from Bovee (1978)

The output is a matrix showing the total surface area of the stream over different combinations of hydraulic variables (see Table 3.1). The matrix is two-dimensional in its simplest form (e.g. depth *versus* velocity) but may be multi-dimensional, considering the interaction of numerous variables such as depth, flow, substratum and cover.

Table 3.1 Example section of a depth-velocity matrix

Depth (m)	Velocity (ms^{-1})				... etc
	< 0.15	0.15-0.30	0.30-0.45	0.45-0.60	
< 0.30	585	78			
0.30-0.45	270	141		123	
0.45-0.60	87	114	96	132	
0.60-0.75	18	87	69	27	
... etc					

The figure in the upper left hand corner of Table 3.1 indicates that $585 \text{ m}^2\text{km}^{-1}$ of stream holds a combination of depth < 0.3 m and velocity < 0.15 ms^{-1} . This figure represents the summation of such patches throughout the reach; not necessarily a 585 m^2 block.

The basic assumption during this stage is that fish select the most favourable conditions within a stream: sub-optimal habitats will be exploited but with an increasingly lower

probability compared to the optimal habitats. Observational or experimental studies (e.g. electro-fishing or direct SCUBA observations) are used to find the relative utility of habitat conditions, in the form of preference curves (Figure 3.2).

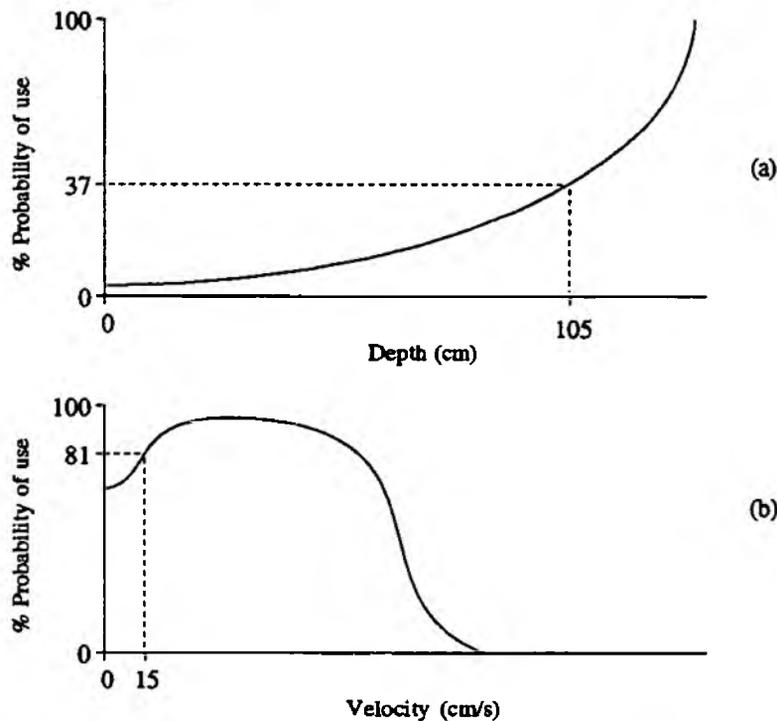


Figure 3.2 Habitat evaluation graphs for adult small-mouthed bass (Bovee 1978).

Figure 3.2 shows that:

- (a) Probability of small-mouthed bass inhabiting a depth of 105 cm = 0.37
- (b) Probability of small-mouthed bass inhabiting a velocity of 15 cm s⁻¹ = 0.81

The probability of bass inhabiting a region of 105 cm depth and 15 cm s⁻¹ velocity is therefore 0.37 x 0.81 (0.30). If the substratum is then studied, and found in this instance to have a probability of use of 0.90, the composite probability of use becomes 0.37 x 0.81 x 0.90 (0.27). Several habitat features could be combined in this way, provided that relationships such as those in Figure 3.2 are known.

Weighted Usable Area

The final stage of IFIM is the prediction of Weighted Usable Area (WUA): defined as 'the total surface area having a certain combination of hydraulic conditions, multiplied by the composite probability of use for that combination of conditions'. In the hypothetical example above, if 305 m² of the reach had the cited feature combinations, the estimated value of that area would be equivalent to 82.4 m² (0.27 x 305 m²) of optimum habitat.

IFIM has been criticized because of its simplifying assumptions; but is a valuable tool for prediction of hydraulic habitat changes for both fish and invertebrates. Its incorporation into RCS methodology would be difficult because of the recurrent cost of detailed transect

measurements; and the initial cost of research towards habitat utility curves. However, it is possible that a less quantitative version could be developed if the records and maps of river stretches enabled proportions of each habitat to be estimated, and this information was combined with existing knowledge of fish species' ecology. Visual recording of the occurrence of functional habitats could provide much of the information required for invertebrates.

3.1.2 Habitat assessment and scoring systems

An alternative approach to IFIM is the measurement and statistical testing of as many environmental variables as possible which might define the habitats of a species or life-stage, together with observations on the time spent in different habitats by target species. 'Habitat' generally refers to the immediate physico-chemical and biological conditions (e.g. channel form, temperature, predation, food availability, competition) but these are influenced by catchment-level factors such as hydrology, geomorphology, topography and land use; and all need to be incorporated into a habitat model. Table 3.2 is a list of habitat categories produced for modelling Welsh rivers (Milner *et al.* 1985).

Table 3.2 Examples of habitat attributes in evaluation schemes (Milner *et al.* 1985)

a) catchment attributes

Hydrology	Geomorphology	Water chemistry
Altitude	Average daily flow	pH
Geology	Average seasonal flow	Hardness
Catchment area	Pattern	Alkalinity
Total channel length	Extreme flow variation	NO ₃ - nitrogen
Drainage density	Stability of flow regime	Phosphorus
Mean basin length	Precipitation	Dissolved solids
Mean basin slope		Conductivity
Forest ratio		Temperature

b) site attributes

Width	Bank erosion	Riffle/pool ratio
Depth	Water surface area	Velocity
Substrate composition	Volume	Gradient
Sinuosity	Flow type	Fish food abundance
Instream cover (debris, rocks, macrophytes)		Fish food diversity
Bankside cover (undercut banks, overhanging vegetation, tree roots)		

Three levels of measurement of physical site attributes can be used:

- Visual analysis: inherently subjective, pragmatic response to limited resources.
- Semi-quantitative: transect data, subjectively assessed for habitat quality.
- Quantitative: detailed study (of transects, mapping) against numerical criteria.

This approach is more amenable than IFIM to incorporation in RCS methodology, by a combination of field data recording and desk addition of catchment geomorphology, hydrology and water quality. The habitat requirements of individual fish species would first need to be established (e.g. Sections 4-7 of this report) and then incorporated into RCS survey for the river systems appropriate for each species. There would have to be at least three classes of river system (salmonid, chub/dace, roach/bream).

3.2 Aquatic invertebrates

3.2.1 Context

There are four main factors which affect stream individual macroinvertebrate species and their community structure:

1. Water quantity. Low flows and flood events are the extremes of a naturally-variable supply of water to the stream. Discharge is also altered by man: through abstraction; impoundment; and cultural modification of catchment hydrology.
2. Water quality. Acidity, solutes, biological oxygen demand *etc.* vary between and within streams. Water quality is affected by cultural consequences such as acidification, eutrophication and urban runoff; and by chemical pollution *per se*.
3. Species interactions. Predation, competition, commensalism *etc.* operate between stream invertebrates – and with other species – to produce communities which are not simply related to individual species' responses to the environment.
4. Physical environment. Flowing water is a major geomorphic influence, which produces diverse physical conditions through erosion-deposition and sorting of sediment. Aquatic macrophytes also contribute to the physical environment of macroinvertebrates but are in turn influenced by hydraulics and sedimentology.

Each of these factors present challenges for the conservation of macroinvertebrates, in response to demands (e.g. water supply and disposal, recreation, land drainage, flood relief) or incidental influences (e.g. pollution, development) on the stream.

Water quantity

The importance of water quantity to life in regulated rivers has been addressed by the use of Instream Flow Incremental Methodology (IFIM: Bovee 1982). Habitat availability under possible discharge regimes is calculated – for example using the Physical Habitat Simulation system (PHABSIM: Milhous *et al.* 1981, 1989) – to provide recommendations in the face of impoundment, flow augmentation or stream/groundwater abstraction. IFIM has most frequently been applied to selected fish species; other groups have rarely been considered (e.g. Hippopotamus: Gore *et al.* 1992) but there are no fundamental barriers to its wider application.

IFIM requires quantitative information on stream morphometry and habitat use (see also Section 2.1.1); both of which can be difficult or expensive to obtain. An alternative to exhaustive channel measurements is the use of frequency estimates based on geomorphological principles (Singh and Broeren 1989). Riffle species are probably impacted soonest by reduced discharge (Bovee 1982). Gore (1978) studied the instream flow requirements of 37 riffle invertebrates and chose *Rhithrogena hageni* as an indicator whose tolerance most closely matched the conditions for highest community diversity. He proposed a method (later formalized as IFIM) for setting minimum flows to safeguard diversity, based on the requirements of the indicator species. Inclusion of invertebrates in issues of water quantity management is important; but requires habitat information for a wide range of species, or a sound scientific basis for the selection of indicators.

Water quality

Macroinvertebrates have been the basis for a series of methods for the biological assessment of water quality. Biotic score systems have been developed and improved

(Woodiwiss 1964, Chandler 1970, Chesters 1980, Armitage *et al.* 1983, De Pauw and Vanhooren 1983, De Pauw and Roels 1988); but sensitive taxa are often characteristic of upland streams, leading to misclassification of clean lowland rivers as 'polluted' (Jones and Peters 1977).

The River Invertebrate Prediction and Classification System (RIVPACS: Wright *et al.* 1989, Cox *et al.* 1991) estimates the macroinvertebrate fauna to be expected at a site from a set of environmental variables; and this can then be compared with results from sampling. A similar project was carried out on Australian streams by Storey *et al.* (1990). Shortfalls in the actual species list may be due to poor chemical water quality, but may also reflect physical habitat conditions at the site. The set of variables used to predict species presence includes 'continuous' measures such as channel dimensions and streambed particle size; but does not allow for the richness of specific habitats, including macrophytes. Simple measures of habitat richness have been included in the interpretation of biotic indices (Extence *et al.* 1987) and more detailed habitat investigations are being carried out at a subset of the sites used for the RIVPACS database (Wright *et al.* 1992). Macroinvertebrates remain the most usual basis for biological assessment of water quality: the increasing need for appraisal against quality targets means that accurate information on their habitat relationships is required.

Species interactions

Predation by fish (Hemphill and Cooper 1984, Schofield *et al.* 1988) and by other macroinvertebrates (Peckarsky 1981, Hildrew and Townsend 1982) affects abundance of prey species. There are also indirect effects on distribution, through predation-driven behaviour of prey species (Peckarsky 1980, Walton 1980) and sometimes predators (Malmqvist and Sjöström 1984, but not Peckarsky and Dodson 1980). As in other ecosystems, interspecific competition is intuitively likely but has been hard to demonstrate. Hildrew *et al.* (1984) found some evidence of competition – decline of population densities, niche width and niche overlap with increasing species richness – in Ashdown Forest streams, but were forced to describe the conclusions as 'tentative'. Where predation is sufficiently important, prey species may not be limited by food or other habitat resources, and thus not compete (Paine 1966).

Commensal and mutualistic interactions are probably less frequent than predation but certainly lead to habitat specificity. The chironomid *Epoicocladus flavens* lives only in association with *Ephemera danica* (Tokeshi 1986a, 1988); and thus assumes the substratum requirements of its host. Similarly, ciliate Protozoa are commonly found on plants and larger animals such as Trichoptera (Baldock 1986) and Ephemeroptera (Tokeshi 1988). Mutualism can influence joint habitat requirements: the growth of *Spongilla lacustris* is greatly reduced in darkened conditions, by deprivation of its algal symbionts (Frost and Williamson 1980).

The variety of species interactions, with lotic food-web complexity (e.g. Figure 7.2), means that streams cannot be managed to produce an off-the-shelf assemblage of macroinvertebrates. Appropriate management can, however, encourage a rich community by the provision of diverse habitats.

Physical environment

One approach to understanding stream communities is to try and study their determinants in isolation, including characteristics of the physical environment. Species composition is obviously influenced by substratum grain size, flow velocity and stream temperature etc. but quantification of such effects is harder. Experimental manipulation to reduce the number of variables may be difficult (e.g. substratum / velocity / depth); or produce results which do not correspond to natural situations. Most usually, more or less extensive surveys of communities

and their environment have been carried out; to provide data for statistical discrimination of the effects of multiple factors.

Sometimes it is unclear which stream characteristics should be measured (and how best to measure them) but a broader understanding is being developed. Communication between disciplines has been a strong feature of stream science (Cummins 1992); and increasing collaboration of biological and physical scientists has led to consideration of community structure in the context of stream hydraulics (e.g. Statzner and Higler 1986). Flow rates and boundary layer effects have been classified (Davis and Barmuta 1989); and studied for their effect on benthic macroinvertebrates (Statzner 1981) and micro-invertebrates (Statzner and Holm 1982, Silvester and Sleigh 1985). Research has been aided by techniques for quantitative measurement of hydraulic conditions by non-specialists (e.g. Statzner and Müller 1989).

An alternative approach is to look for patterns in community structure, returning to a more descriptive style of research. For current purposes in river conservation it may be sufficient to identify environmental units (types of river, reach or habitat) in terms of observed biological communities; then to look at the management required for maintenance/enhancement of those units, conserving the communities by default.

Systems for classification of whole streams (e.g. Shelford 1913, Ricker 1934) and longitudinal zones within a stream (reviewed by Illies and Botosaneanu 1963, Botosaneanu 1979, Statzner and Higler 1986) have been proposed for a long time. Pennak (1971) discussed the shortcomings of whole-stream descriptions, and of zonation systems based on individual indicator taxa. He favoured the stream reach as an elemental unit for classification, using 13 physical, chemical and vegetation parameters to describe the habitats of species 'clusters'. This approach has been refined in a number of recent classifications; where improved computing power has allowed multivariate statistical treatment of many reaches and variables.

Multivariate methods have been used to classify river (reach) types on the basis of macroinvertebrates (Wright *et al.* 1989, Storey *et al.* 1990) or macrophytes (Holmes 1989); and have also been applied to ditches (Verdonschot 1992a) and standing water (Verdonschot 1992b). A classification of drainage channels, based on aquatic Coleoptera, was developed by Foster *et al.* (1990) to identify sites of particular conservation value and guide management recommendations. Multivariate analysis also seems to offer a means to classify 'qualitative habitats' (substratum/flow categories, macrophyte species etc.) according to their invertebrate species complement; but work at this 'within-reach' level (e.g. Bournaud and Cogerino 1986, Smith *et al.* 1991) is less frequent than at the 'between-reach' level (e.g. cases above).

This review

The objective of this section is to review some of the information on relationships between stream macroinvertebrates and physical habitat, with particular emphasis on habitat classification. Physical habitat includes aquatic macrophytes and allochthonous plant material, which are also discussed as a food resource.

3.2.2 Background

Physical features of the channel which contribute to landscape have always been on the agenda of river corridor surveys. Macrophytes have also been surveyed to a varying degree as direct targets for conservation. Both physical and botanical characteristics strongly influence the macroinvertebrate community, but their value as habitat features for survey is presently limited. A set of 'functional habitats' are needed for recording, which each contribute to habitat value (towards invertebrate abundance or species richness) and which can be consistently identified.

Some studies have looked at the species abundance and richness of a single habitat (Williams 1984, Strommer and Smock 1989), or compared a limited range of habitats (Percival and Whitehead 1929, Cummins and Lauff 1969, Rooke 1984, Suren 1991) but have not started with a division of the whole. Attempts have been made to partition the total habitat of the stream channel, to ensure that species inventories are complete in biological surveys (e.g. Brooker 1982: see Table 3.3). Samples have then often been pooled for species identification, losing information on habitat selectivity (Ormerod and Edwards 1987: riffle, margin and slow run). An alternative strategy has been to take samples from habitat groups (Rutt *et al.* 1989: riffles, margins) and then to interpret the results in terms of more detailed habitat structure.

Table 3.3 Habitat types on the River Teifi (Brooker 1982)

Habitat	Physical description
Riffle	High current velocity, disturbed surface
Fast run	Similar current velocity to, but deeper than riffle
Slow run	Similar to fast run, but with reduced current velocity
Pool	Discrete area between faster reaches; velocity reduced, depth variable
Slack	Shallow bankside area of much reduced current velocity, generally silty
Backwater	Area of minimal current velocity, partially isolated from channel during low flow
Tree roots	Submerged fibrous system of alder, ash, sycamore and willow in deep water
Grass roots (<i>Phalaris</i>)	Submerged fibrous systems of bankside stands
<i>Ranunculus penicillatus</i>	Extensive stands in regions of low current velocity, usually at margins of channel
<i>Callitriche hamulata</i>	As above
<i>Potamogeton natans</i>	As above

Table 3.4 Habitat types on the Acheron River (Barmuta 1989)

Habitat	Summer appearance	Winter appearance
Riffles	Fast, broken water, >10 cm deep; coarse substratum of pebbles and cobbles	As for summer
Pebble beds	Flowing, broken water, <10 cm deep; substratum mostly pebbles of smaller apparent size than riffles	Fast broken water over summer 'pebble' and 'exposed' habitats
Cobble pool or run	Slow, smooth-flowing water >10 cm deep; coarse substratum of pebbles and cobbles; little surficial silt or organic matter	Faster but still smoothly flowing water; >10 cm deep; substratum as for summer
Silted pebbles	Slow or still water; coarse substratum of pebbles >80 % covered by fine sediments and organic matter	Absent
Exposed pebbles	Shallow, 0.5-2.0 cm deep trickles or puddles of water; substratum mostly pebbles with tops exposed	Absent
Silted sands	Still or slowly flowing water; sandy surficial sediments >80 % cover of silts and organic materials	Absent
Clean sands	Still or slowly flowing; sandy surficial sediments <20 % cover of silts or fine organic material	As for summer
Mixed sands	Still or slowly flowing water; surficial sediments a mixture of organic and sandy materials	As for summer

Barmuta (1989) studied the macroinvertebrate distribution between classes of physical substrate in an Australian upland stream. Substrate classes were defined in a way applicable to survey (visually distinguishable) and included descriptions of their appearance under summer

and winter flows (Table 3.4). Distinct community differences were found between erosional and depositional substrate types, with a large proportion of the variation accounted for by velocity, mean particle size and depth. Within the two major habitat groups the community was heterogeneous, but there were no marked discontinuities to indicate further functional habitats. Erosional and depositional habitats were also distinguished by Cummins *et al.* (1984) in terms of the dominant invertebrate feeding guilds (Table 3.5).

Table 3.5 Habitat classes and invertebrate adaptations (Cummins *et al.* 1984)

Habitat	Dominant habits	Dominant feeding groups	Dominant organic food resource
Erosional (riffles, rapids, cascades, runs, glides)	Clingers	Scrapers	Periphyton
		Filtering collectors	FPOM (sloughed periphyton, transport-suspended and bed-load)
	Swimmers	Gathering collectors	Depositional FPOM
Depositional (pools, margins, off-channel, side channel)	Burrowers and crevice dwellers	Gathering collectors	Depositional FPOM
		Shredders	Depositional CPOM and macrophytes
	Sprawlers	Gathering collectors	Depositional FPOM
Depositional (pools, margins, off-channel, side channel)	Burrowers	Shredders	Leaf packs
		Gathering collectors	Depositional FPOM
	Climbers	Shredders	Leaf packs, wood
		Shredders	Vascular hydrophytes
		Piercers	Macroalgae

Replicated sampling from a non-exhaustive list of particulate and vegetative potential habitats was carried out by Bournaud and Cogérino (1986), who studied the submerged banks of a canalized reach of the River Rhône. They concluded that the *a priori* definition of 12 potential habitats (*microhabitats prospectés*, Table 3.6) was validated by macroinvertebrate distribution, subject to varying overlap within three wider habitat classes of erosion, sedimentation and vegetation.

Table 3.6 Habitat types on the River Rhône (Bournaud and Cogérino 1986)

Boulders (25-100 cm Ø)	Silted gravel	Branches <5 cm Ø
Stones (3.2-25 cm Ø)	Silted sand	Branches >5 cm Ø
Gravel (0.2-3.2 cm Ø)	Excavation (bare cavity under boulders, roots etc.)	Fibrous roots
Sand (600 µ-0.2 cm Ø)	Roots <5 cm Ø	Algae

Smith *et al.* (1991) studied the macroinvertebrates of 42 potential habitats on the River Welland in NRA Anglian Region (Table 3.7). Analysis using TWINSPAN (Hill 1979) showed 20 functional habitats (Table 3.8), which were used to produce a surveyors' habitat checklist (Table 3.9). Some interpretation of the functional habitat list was required: for example the shoots and roots of emergent macrophytes were combined for survey due to their inevitable co-

occurrence; 'rocks in pool' was not included because it was an artificial feature; and sand was characterized only by absence of species, so figured only as the sole physical substrate at a site. Functional habitats were similar on a second river in Anglian Region, with different water chemistry, macrophyte and macroinvertebrate species, which indicated potential for a broadly-applicable list of functional habitats (Harper *et al.* 1992).

Table 3.7 Potential habitats on the River Welland

<i>Cladophora</i> sp. (pool)	<i>Potamogeton pectinatus</i> (run)	<i>Phalaris arundinacea</i> (margin)
<i>Cladophora</i> sp. (run)	<i>P. pectinatus</i> (riffle)	<i>Agrostis stolonifera</i> (margin)
<i>Enteromorpha</i> sp. (pool)	<i>Potamogeton perfoliatus</i> (run)	<i>Rorippa amphibia</i> (margin)
<i>Enteromorpha</i> sp. (run)	<i>Ranunculus penicillatus</i> (run)	Silt (pool, with leaf litter)
<i>Potamogeton natans</i> (pool)	<i>R. penicillatus</i> (riffle)	Silt (pool, without leaf litter)
<i>Nymphaea alba</i> (pool)	<i>Schoenoplectus lacustris</i> (run)	Sand (run, u/s riffle)
<i>Nuphar lutea</i> (pool)	<i>Glyceria maxima</i> (margin, shoots)	Sand (run, d/s riffle)
<i>N. lutea</i> (run)	<i>G. maxima</i> (margin, roots)	Sand (margin, point bar)
<i>Elodea canadensis</i> (pool)	<i>Sparganium erectum</i> (margin, shoots)	Gravel (run, u/s riffle)
<i>E. canadensis</i> (run)	<i>S. erectum</i> (margin, roots)	Gravel (run, d/s riffle)
<i>Fontinalis antipyretica</i> (run)	<i>Schoenoplectus lacustris</i> (margin, shoots)	Riffle substrate (set A)
<i>F. antipyretica</i> (riffle)	<i>S. lacustris</i> (margin, roots)	Riffle substrate (set B)
<i>Potamogeton lucens</i> (run)	<i>Carex acutiformis</i> (margin, shoots)	Riffle substrate (set C)
<i>Myriophyllum spicatum</i> (run)	<i>C. acutiformis</i> (margin, roots)	Rocks (c. 30 cm Ø, pool)

Table 3.8 Functional habitats on the River Welland

<i>Elodea canadensis</i> (pool)	<i>Cladophora/Enteromorpha</i> spp. (pool)	Silt (pool, leaf litter)
<i>F. antipyretica</i> (riffle)	Emergent macrophytes (margin, shoots)	Silt (pool, no leaf litter)
<i>Potamogeton lucens</i> (run)	Emergent macrophytes (margin, roots)	Sand
<i>Nuphar lutea</i> (run)	<i>Phalaris arundinacea</i> (margin)	Gravel (run, u/s riffle)
Other submerged macrophytes	<i>Agrostis stolonifera</i> (margin)	Gravel (run, d/s riffle)
<i>Potamogeton natans</i> (pool)	<i>Rorippa amphibia</i> (margin)	Riffle substrate
<i>Nymphaea/Nuphar</i> (pool)	Rocks (c. 30 cm Ø, pool)	

Table 3.9 Habitat checklist for the River Welland

Gravel	Run – <i>Nuphar</i>	Margins – 'reeds'
Riffle	Pool – <i>Nuphar</i> or <i>Nymphaea</i>	– <i>Rorippa</i>
– with <i>Fontinalis</i>	– <i>Elodea</i>	– <i>Phalaris</i>
Silt – with leaf litter	– <i>Cladophora / Enteromorpha</i>	– <i>Agrostis</i>
– without leaf litter	Other submerged plants	
If none above, sand ...	– how many (for information) ?	

The functional habitats of varied river types are currently being investigated in a national context (NRA R&D Project 346 – Project Leader P. Barham, Anglian Region). The main issues are to identify additional habitats absent from the Anglian Region rivers; to find out how generalized the definitions of functional habitats can be; and to give information on the relative importance of habitats to different river types. A full list of potential habitats is being studied on

each of ten river reaches (Table 3.10), representing the dominant river types identified by the IFE River Communities Project (Wright *et al.* 1984, 1989).

Table 3.10 Rivers studied currently by NRA R&D Project 346

River (NRA Region)	Reach (Grid references)	River (NRA Region)	Reach (Grid References)
Dove (S-T)	SK 084 665 - SK 146 504	Ichen (S)	SU 523 325 - SU 470 233
Swale (Y)	NY 885 015 - NZ 146 007	Ouse (Y)	SE 467 621 - SE 591 455
Wansbeck (N)	NY 996 844 - NZ 119 850	H. Avon (Wes)	SU 163 174 - SZ 158 933
Torridge (S-W)	SS 324 178 - SS 542 064	Mimram (T) ¹	TL 193 207 - TL 282 134
Teifi (Wel)	SN 684 628 - SN 217 437	Smite (S-T)	SK 690 262 - SK 773 427

Note: ¹ Subject to summer flow – may be replaced by another river of same type to avoid disturbance

The Institute of Freshwater Ecology have sampled potential habitats at 76 sites on 32 of the rivers included in their River Communities Project database (Wright *et al.* 1992). Twelve samples have been taken from each site, without explicit replication of potential habitats. The IFE included underlying substratum in macrophyte samples, whilst the NRA work treats the rootstock of macrophytes separately. The studies being carried out by the NRA and IFE are of complementary scope and detail, and will provide a sound scientific basis for the practical inclusion of in-stream habitat features in river corridor surveys.

3.2.3 Particulate substrata

Particle size is probably the physical habitat variable for which most data is available – Leland *et al.* (1986) were able to find information for each of 21 common taxa in a Californian stream. The benthic fauna differs between substrates of dissimilar particle size (e.g. Doeg *et al.* 1989, Smith *et al.* 1991). Differentiation of linear or non-linear community responses to particle size has been difficult in many studies, due to *a priori* definition of substrate size categories. Some cases have suggested that a series of discrete benthic community types exist, in terms of associated substratum particle size (Thorup 1966, Reice 1974). For the most part however, a gradual change in species composition has been shown with the transition from fine to coarse sediment (Rabeni and Gibbs 1980, Sheldon and Haick 1981, Barnuta 1989).

Discrete communities may not exist in relation to particle size *per se*, but the latter is discontinuously variant in the stream channel. Transitions between riffle and pool regimes of substrate are often spatially abrupt, even though depth and flow rate can be normally-distributed (Singh and Broeren 1989). This habitat patchiness might produce community patchiness even for monotonous variation of species with substratum (Figure 3.3).

The American Society of Civil Engineers (ASCE) combined hydraulic and biological information in a classification of bed material (ASCE 1992: see Table 3.11); and reviewed many of the issues relevant to each bed type. The authors were referring primarily to stream types but the macroinvertebrate communities respond in a similar way to local bed characteristics. Their boulder-cobble category corresponds mainly to mountain streams which exhibit a 'stair-step' long profile; analogous conditions may occur in the headwaters of lowland streams, especially if bed material is augmented by coarse woody debris. The remaining categories occur on most rivers, where their relative importance is influenced by geology and flow regime.

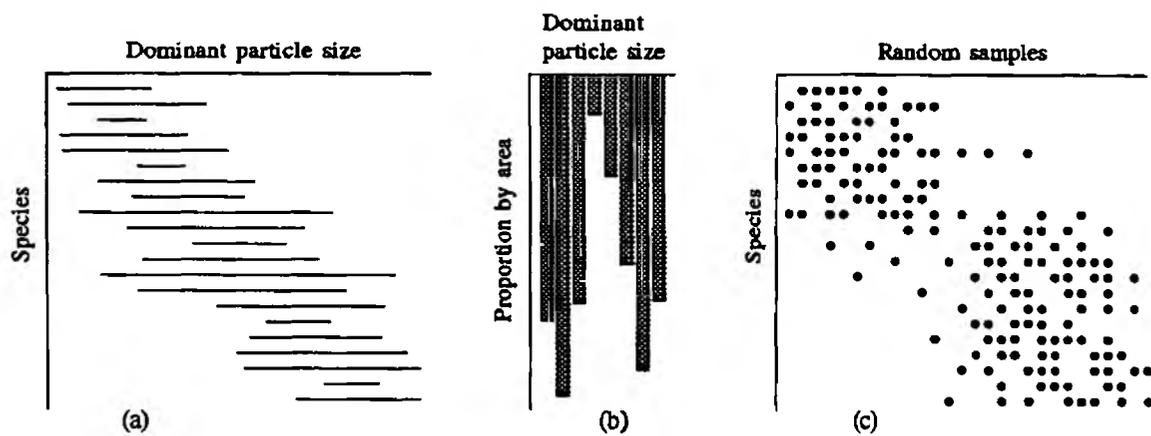


Figure 3.3 Conceptual diagrams: 'random' particle-size tolerances (a) could still produce distinct communities (c), if the distribution of dominant particle-size is not unimodal (b).

Table 3.11 Example of a bed-material classification (ASCE 1992)

Bed type	Particle size (mm)	Relative frequency of bed movement	Typical macroinvertebrate		Fish use of bed sediments
			Density	Diversity	
Boulder-cobble	≥ 64	Rare	High	High	Cover, spawning, feeding
Cobble-gravel	2-256	Rare to periodic	Moderate	Moderate	Spawning, feeding
Sand	0.062-2	Continual	High	Low	Feeding (off-channel, fine)
Fine material	<0.062	Continual or rare	High	Low	Feeding

Some taxa are strongly associated with cobble substrata in streams (e.g. crayfish: Capelli and Magnuson 1983, Miller 1985, Elminthidae: Brown 1987) and the high abundance of invertebrates on riffle substrata (typically cobble-based) has been established for a long time (Wene and Wickliff 1940, Pennak and Van Gerpen 1947). In most cases the highest species richness is also associated with coarse sediment (Pennak 1971, Cummins 1975, Hart 1978, Gore and Judy 1981). Williams and Mundie (1978) looked at macroinvertebrate utilization of artificial gravel beds, with 11.5 mm, 24.2 mm and 40.8 mm diameter. They found maximum abundance in 24.2 mm gravel, while diversity was greatest in the largest substratum. Beds dominated by large particles generally include a range of finer sediment and organic matter which encourages both abundance and diversity of species (Hynes 1970). Williams (1980) observed such a result with experimentally-manipulated substrata, including a heterogeneous substratum with an upper layer of coarse material. These are the conditions which occur in established riffles, through the process of armouring (Jain 1990).

Smith *et al.* (1991) found that gravel (of *c.* 0.5-2.0 cm Ø) was a distinct macroinvertebrate habitat on the Rivers Welland and Wissey in NRA Anglian Region. They also found differences between gravel at the head and tail of riffles, which were not explicable solely in terms of drift. Gravels are important as fish spawning sites, notably of salmonids but also of some key coarse fish such as chub *Leuciscus cephalus* (Wheeler 1978). The known requirements of a range of species were reviewed by Wesche (1985) who gave a particle size range of 0.6-7.6 cm, which is smaller than that found as the dominant element of most riffles.

The 'hyporheic zone' of interstitial spaces in cobble or gravel-based stream beds is an important habitat for invertebrates (Stanford and Gaufin 1974). Waringer (1987) found Trichoptera larvae down to 1 m in a gravel bed, with maximum numbers of early-instar *Sericostoma* at 20-60 cm. The habitat value of the hyporheic is generally reduced by large amounts of fine sediment (Nuttall 1972, Boles 1981) although organic matter has been found to be beneficial (Williams and Mundie 1978, Milner *et al.* 1981). Distinct communities can be found in the hyporheic zone (e.g. of Limnohalacaridae: Husmann and Teschner 1970), especially when the stream geomorphology produces zones of upwelling and downwelling (Dole-Olivier and Marmonier 1992).

Sand is usually poor as a habitat in terms of both abundance and diversity for macroinvertebrates > c. 1.0 mm (Pennak 1971, Bournaud and Cogerino 1986, Smith *et al.* 1990). Wagner (1984) modified a portion of stream-bed to be homogeneous sand: the numbers of many taxa declined but some (e.g. Ptychopteridae, *Centropilum luteolum*) became more abundant. The specialized meiobenthos of mostly smaller animals may be very abundant; though still species-poor (Whitman and Clark 1984, Soluk 1985) and not extending to such depths as in the gravel hypopetric environment (15-30 cm: Strommer and Smock 1989). Sand is usually the least stable of riverine sediments on the time-scale of macroinvertebrate life-cycles (Peeters and Tachet 1989) but deposits associated with flow obstructions such as woody debris can accumulate organic matter (Newbold *et al.* 1981). They then support richer invertebrate communities (Anderson and Day 1986) and may become vegetated. Terrestrialization of sand on point bars also occurs, as an element of meander migration.

Brown and Brussock (1991) found that riffle macroinvertebrates of the Illinois River were more species-rich and abundant than those of bedrock-dominated pools. Gore (1985) also stated that pools do not provide large amounts of suitable substratum for macroinvertebrates. This contrasts with the silt of pools studied by McCulloch (1986) and Smith *et al.* (1990), which held comparable or greater species richness and biomass to riffles. The main difference is probably between lowland and upland streams; and the key habitat feature is detritus-rich silt, stable for much of the summer, rather than pools *per se*. Silt with and without leaf litter held distinct macroinvertebrate assemblages on the River Welland (Smith *et al.* 1991). Some species were limited to litter-free silt, which they suggested was an effect of reduced pressure there from mechanically-disadvantaged predators.

On rivers to which it is appropriate, the key factor in maintenance or restoration of substratum spatial diversity is the riffle system. Restoration of coarse material to managed rivers is a successful technique for fishery enhancement (Mih 1978) and also macroinvertebrate conservation (Humphreys 1991) but coarseness of the introduced load is important (Boles 1981). Methods for determining progress of the macroinvertebrate community were discussed by Gore (1985) and this is the usual limit of post-restoration appraisal. Some macroinvertebrate species require deposition of sediment on introduced cobbles (Gore and Johnson 1980: cited by Gore 1985) but excessive sedimentation is harmful (Chutter 1969, Luedtke *et al.* 1976, Boles 1981); further study is therefore needed on the conditions for import and retention of fine sediment to new structures (Youdan, T. personal communication).

3.2.4 Aquatic macrophytes

Habitat value

Macrophytes provide a major component of productivity in many stream types (reviewed by Fisher and Carpenter 1976). In small, shaded reaches few macrophytes may succeed, typically mosses; but elsewhere they are often abundant and species-rich.

Statistical correlations between the species richness of macrophytes and macroinvertebrates (Jackson *et al.* 1979, Palmer 1981, Ormerod *et al.* 1987) need not indicate causal relationships. Friday (1987) found a correlation between invertebrate and plant species richness in ponds; but after accounting for the effect of pH on both, it was no longer significant. Stronger evidence has been obtained in studies of selected taxa. For example, Cuppen (1983) found that two of three *Hygrotus* spp. (Dytiscidae) were more abundant in macrophyte-rich waters; and Jeppesen *et al.* (1984: cited by Sand-Jensen *et al.* 1989) found areal densities of simuliids and chironomids increased several-fold in the presence of macrophytes. A seasonal correlation between abundances of *Potamogeton pectinatus* and four invertebrate species was observed by Bergey *et al.* (1992). They showed definite ecological relationships between the invertebrates and the phenology (growth, canopy and senescence phases) of the macrophyte.

Plants act as habitat features for stream macroinvertebrates in several main ways:

- The living tissue is a food resource for species which shred, mine or pierce the plant. Some invertebrates also use leaf or stem segments as case material.
- Macrophytes provide an extension of the physical substrate; and a large surface for periphyton, grazed by many invertebrates.
- Instream plant litter is a food resource for detritivores, with a similar process of decomposition to allochthonous material (see section discussing leaf litter).
- Both aerial and submerged portions are used as sites for oviposition; and some plants provide a route for emergence of insects.
- Macrophytes can provide a refuge from predation and adverse flow conditions. Some invertebrates also obtain oxygen from roots, in otherwise anoxic sediment.

Direct consumers of living plant material are usually a small proportion of the macroinvertebrate community, with most use of senescent plants (Soszka 1975). Dvorak and Best (1982) found direct consumers formed 0.6% of invertebrate abundance in Lake Vechten; and that together with miners and filterers, consumption was 0.03% of daily primary production. In streams, the use of living plants as food may be even less, and restricted to lentic habitats (e.g. Trichoptera: Elliott 1969, Mackay and Wiggins 1979 and Ephydriidae: Berg 1950). Mining chironomids (particularly Chironominae) are most abundant on emergent plants (Dvorak and Best 1982), although they are usually filter feeders rather than direct consumers of the host plant (Walshe 1948). A specific community of nematodes is found in the roots/rhizomes of aquatic plants (Prejs 1977) and there are individual species associations (Prejs 1986). The larvae of many Hydroptilidae pierce plants (filamentous algae) for food (Wallace *et al.* 1990) but this mode of feeding is uncommon (Rooke 1986b). Plant segments are used for case material by many Trichoptera (Wallace *et al.* 1990) and some Lepidoptera (Hasenfuss 1960: cited by Verdonschot 1992a).

Vegetation is important to periphyton grazers such as Naididae (Learner *et al.* 1978, Bowker *et al.* 1985), chironomids (Tokeshi 1986b), chydorid Cladocera (Fairchild 1981) and gastropods (Lodge 1985). Diatoms of the periphyton are also needed as case material for some chironomids (Fairchild 1981). The proportions of periphyton types (e.g. filamentous green algae and diatoms) can differ between macrophyte species, producing a diverse environment for selective grazers (Lodge 1986). Macroinvertebrates make much more use of the periphyton than of the macrophytes. Kairesalo and Koskimies (1987) found consumption by oligochaetes and gastropods was 22-45% of daily periphyton production (*cf* 0.03% of macrophyte production: Dvorak and Best 1982). Cattaneo and Kalff (1980) estimated that epiphyte production was almost as much as that of the macrophytes, which makes grazing of epiphytes an important link between primary producers and the animal community (Cattaneo 1983).

The seasonal abundance of smooth substrate which some macrophytes provide is of benefit to macroinvertebrates such as some leeches and gastropods. Lodge (1985) studied the distribution of 13 gastropods and 10 macrophytes: he proposed that restriction of *Acroloxus*

lacustris to *Nymphaea alba* and emergent species was due to its need for a broad substrate for attachment and locomotion. Rooke (1984) found no community difference between *Potamogeton amplifolius* (broad leaves, low habit) and the stone substrate, suggesting that it was used as an 'extension' of the stream bed. A further habitat feature is provided by the meniscus formed where macrophytes reach the water surface. This may be used by *Anopheles* larvae as a refuge from predation, being less visible to fish and Hemiptera (Bergey *et al.* 1992).

Dytiscidae use a range of macrophyte species for oviposition, either on the surface of shoots and roots (*Agabus*: Jackson 1958) or within the shoots (*Ilybius*: Jackson 1960). Many Odonata lay their eggs on or within macrophytes, with varying degrees of specificity (Corbet 1980). Oviposition was suggested as a particular value of mosses in faster water by Glime and Clemons (1972). Plants provide a passage to the water surface for emerging insects (McGaha 1952, Gaevskaya 1966: cited by Rooke 1984). Rooke (1984) found that plants supported a higher proportion of species with aerial life stages than stones; which may be related to their use for subsequent emergence.

The intricate structure of some submerged macrophytes (particularly mosses) can provide a refuge from predation and flow (Malmqvist and Sjöström 1984, Wellborn and Robinson 1987). Emergent vegetation is chosen as shelter by some *Gerris* species in response to wind or wave action (Spence and Scudder 1980, Spence 1981). Macrophytes can also be an important predation refuge for young fish (Hart, P.J.B. personal communication). As a refuge from anoxia, the larvae and pupae of some Diptera insert their spiracles into the roots of aquatic plants for respiration (Keilin 1944, Houlihan 1969), in which context the density of roots can also be important for leverage.

Habitat categories

Most of the macroinvertebrates associated with aquatic macrophytes are found across a variety of species (Dvorak and Best 1982), though with some degree of preference (Harrod 1964). Broad but incomplete habitat tolerance has also been shown by Rooke (1984, 1986a), Iversen *et al.* (1985) and Engel (1988). Ecological affinities do not always reflect systematics: *Ranunculus penicillatus*, *Potamogeton pectinatus* and *Zannichellia palustris* seem more similar as habitat than *Potamogeton pectinatus*, *P. perfoliatus* and *P. natans*. Wright *et al.* (1992) discussed the value of macrophyte growth forms (habits) for effective study and for their relevance to issues of stream management. The use of ecological, rather than taxonomic, plant categories is needed to study pattern between streams with dissimilar macrophyte communities.

Most aquatic macrophytes are readily categorized according to their habit; as emergent, submerged or floating-leaved. Many species (e.g. *Sparganium emersum*, *Butomus umbellatus*, *Oenanthe fluviatilis*) have leaves which are either submerged or emergent; *Sagittaria sagittifolia* can have linear submerged leaves, long-petiolate floating leaves and sagittate emergent leaves; but one habit usually dominates. Submerged species have been further categorized according to their topology; as those with broad leaves and those with fine or dissected leaves. Marginal herbs have various architectures, mostly different from those of emergent monocotyledons. They are also associated with a distinct set of depth and flow conditions. Mosses and macroalgae typically have growth forms distinct from angiosperms. There are thus seven categories, at least, which may be expected to serve as functional habitats:

- Emergent species (e.g. *Sparganium erectum*, *Glyceria maxima*).
- Floating-leaved species (e.g. *Potamogeton natans*, *Nuphar lutea*).
- Submerged species with broad leaves (e.g. *Potamogeton perfoliatus*, submerged leaves of *Nuphar lutea* and *Sparganium emersum*).
- Submerged species with fine or dissected leaves (e.g. *Myriophyllum spicatum*, *Potamogeton pectinatus*, *Ranunculus penicillatus*).

- Mosses (e.g. *Fontinalis antipyretica*, *Rhynchostegium riparoides*).
- Macroalgae (e.g. *Cladophora glomerata*, *Enteromorpha intestinalis*).
- Marginal species (e.g. *Rorippa* spp., *Phalaris arundinacea*, *Veronica* spp.)

Wright *et al.* (1992) found greater invertebrate family richness on emergent plants than on submerged and floating-leaved plants, which in turn were richer than the substrate, over a large number of British rivers. Wright *et al.* (1983) had previously shown that submerged plants supported more species than the substrate of the River Lambourn. The results in both cases were based on macrophyte samples which included the underlying substrate, on the basis that its habitat characteristics are modified by the plant. Data from Smith *et al.* (1991) show that for one river at least (Table 3.12), the invertebrate richness associated with macrophytes (not including rootstock/substrate) was usually about equal to that of the substrate, except for sand. Communities of silt with or without macrophyte rootstock were quite similar – the greatest qualitative contribution of macrophytes occurred in the water column (Figure 3.4b). Categorization of plants according to growth form was supported by their results: although invertebrate taxa were mostly found on several macrophytes, a number were restricted to each of submerged, emergent and floating-leaved categories (Figure 3.4a). Habit-based macrophyte groups have also been used in more detailed studies of invertebrates. For example, Cuppen (1983) found that *Hygrotus decoratus* and *H. versicolor* were most strongly associated with emergent and submerged macrophytes respectively.

Krecker (1939) suggested that plants with dissected leaves consistently support more invertebrates than those with broad leaves. 'Fine-leaved' plants might provide more surface area for growth of periphyton (Dvorak and Best 1982, Lodge 1986) and attachment of invertebrates (Lodge 1985); capture more fine particulate matter from the flow (Gerking 1957, Rooke 1984); and offer more protection from predation or turbulence (Malmqvist and Sjöström 1984). Experimental evidence (reviewed by Cyr and Downing 1988) is equivocal – many investigations have supported Krecker's hypothesis but some, including Cyr and Downing themselves, found no systematic benefit of fine-leaved species. Data from Smith *et al.* (1991) show some macroinvertebrate species restricted to each of fine- and broad-leaved submerged macrophytes (Figure 3.4c). A large proportion of the 26 restricted species were uncommon but among the taxa found only on broad-leaved plants were gastropods (*Planorbis carinatus*, *P. planorbis*, *P. contortus*, *P. albus*), flatworms (*Polycelis* sp., *Dugesia lugubris*, *Dendrocoelum lacteum*) and leeches (*Helobdella stagnalis*, *Erpobdella octoculata*); all of which might be expected to prefer such a surface.

Table 3.12 Number of taxa found in habitats on River Welland (data: Smith *et al.* 1991)

<i>Cladophora</i> sp.	49	<i>Potamogeton lucens</i>	35	<i>Schoenoplectus lacustris</i>	45
<i>Enteromorpha</i> sp.	39	<i>P. perfoliatus</i>	38	<i>Glyceria maxima</i>	52
		<i>P. pectinatus</i>	39	<i>Sparganium erectum</i>	31
<i>Potamogeton natans</i>	48	<i>Ranunculus penicillatus</i>	45	<i>Carex acutiformis</i>	43
<i>Nuphar lutea</i>	44	<i>Myriophyllum spicatum</i>	36		
<i>Nymphaea alba</i>	24	<i>Elodea canadensis</i> ¹	64	Rifle substrate	68
				Gravel	46
<i>Fontinalis antipyretica</i>	71	<i>Agrostis stolonifera</i>	54	Sand	31
		<i>Rorippa amphibia</i>	49	Silt	49
		<i>Phalaris arundinacea</i>	63		

Notes: Macrophyte samples did not include roots/rhizomes and underlying substrate.

¹ Includes pool samples; but *E. canadensis* does support a diverse community (Nichols and Shaw 1986)

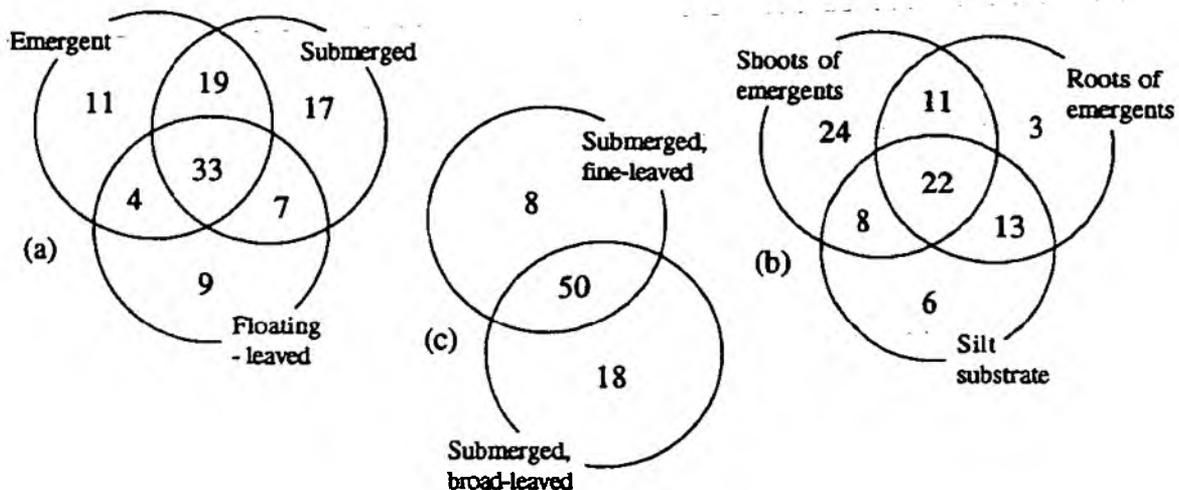


Figure 3.4 Taxon richness of habitats on River Welland (data: Smith *et al.* 1991)

Aquatic mosses are often important components of stream flora, for primary production and nutrient dynamics (Dawson 1973, Meyer 1979). Mosses can support greater invertebrate densities than adjacent gravel substrate (Maurer and Brusven 1983, McElhorne and Davies 1983, Brusven *et al.* 1990). Species richness is also high (Egglshaw 1969, Thorup and Lindegaard 1977, Table 3.12) and positive effects on individual macroinvertebrate species have been shown (e.g. Malmqvist and Sjöström 1984). Suren (1991) demonstrated that in upland New Zealand streams the species associated with bryophytes and gravel were different. Schwank (1984) also found highly specialized communities of smaller invertebrates such as nematodes and rotifers.

The complex structure of a moss stand is a refuge from predation and flow-for-small species, and immature stages (Malmqvist and Sjöström 1984). Fine sediment and organic matter accumulate in mosses (even in strong flows) providing physical substrate and a food resource. According to Percival and Whitehead (1929):

"Thick carpets of moss ... form a dense growth which prevents the easy passage of water between the stems and allows of the accumulation of fine detritus. This kind of bed offers an exceptionally fine medium for the development of a fauna."

Some herbivores, such as *Nemoura*, are reported to feed on both mosses (Hynes 1970) and associated detritus/periphyton (Frost 1942) but most can be expected to use the periphyton. Glime and Clemons (1972) found fewer species and individuals on a plastic imitation of *Fontinalis*. Mosses (with liverworts) also retain water and provide mechanical structure to the hygropetric habitat described elsewhere in this report.

The most characteristic moss of lowland streams in Britain is *Fontinalis antipyretica*. The macroinvertebrate assemblage of *Fontinalis* in riffles on the River Welland was distinct from that of other macrophytes or the substrate (Smith *et al.* 1991); and more species-rich (49, 53) than *Ranunculus penicillatus* (33, 38) or *Potamogeton pectinatus* (22, 35) in similar flow conditions (run, riffle). Other bryophyte species can be as important, especially in upland or colder streams such as the River Tees (Holmes and Whitton 1981). For example, *Rhynchostegium riparoides* is widespread and often abundant (Wehr and Whitton 1983), growing throughout the year in contrast to most other aquatic plants (Kelly and Whitton 1987).

Macroalgae such as *Cladophora glomerata* and *Enteromorpha intestinalis* occur naturally in streams; but their overgrowth is the most visually obvious consequence of the eutrophication

of lowland rivers. It may also be the most ecologically important: by shading of substrates and other macrophytes; alteration of the physical environment; and quantitative modification of trophic relationships in the stream. Macroalgal species now occur at 70 % of all sites with a mean of 40 % bottom cover in lowland mid-eastern English rivers (Harper, D.M. unpublished data).

C. glomerata was associated with high abundance of limited species (pool, *Lymnaea peregere*, run, *Ephemerella ignita* and Orthocladinae spp.) on the River Welland (Smith *et al.* 1991). Macroalgae may provide refuge from predators (Dudley *et al.* 1986, Holomuzki and Short 1988) and are an oviposition site for *Ilybius* (Balfour-Browne 1950). There are some reports of macroalgae as a food resource for invertebrates (Gray and Ward 1979, Behmer and Hawkins 1986) and fish (Greger and Deacon 1988). Feminella and Resh (1991) found that selective grazing on *Cladophora* by the caddis *Gumaga* had a significant effect on algal succession in a Californian stream. Generally however, *Cladophora* is not an important food item (Patrick *et al.* 1983). *Cladophora* is a substrate for epiphytes, which take advantage of its low mucilage production (Chapman 1964: cited by Learner *et al.* 1978), and are subsequently grazed by macroinvertebrates (Dodds 1991).

The margins are less thoroughly studied than the wholly aquatic environment, but may be the first areas to recover habitat complexity in managed channels. Shallow areas may be selected by small fish for food (Bardonnnet *et al.* 1991) or as a refuge from predation (Harvey and Stewart 1991). Schiemer and Spindler (1989) found that shallow margins on the Danube supported more fish fry than neighbouring revetted sections. Semi-aquatic macrophytes contribute to the physical richness of marginal areas for invertebrates, through a variety of habit and position in relation to the water level. Dvorak (1970) found that a marginal stand of vegetation supported a community ranging from semi-terrestrial gastropods to aquatic Heteroptera, varying with distance from the shoreline in a pond. Smith *et al.* (1991) found a large number of macroinvertebrate species in samples from lotic marginal macrophytes (Table 3.12: *Agrostis*, *Rorippa*, *Phalaris*). Their analysis of the data suggested that marginal plant species form more than a single functional habitat; but further study is needed, and is being carried out as part of NRA R&D 346.

3.2.5 Leaf litter

Macroinvertebrates are often significantly associated with leaf litter (henceforth 'litter'), with evidence for individual species (*Eisenia spelaea*: Omodeo 1984) as well as species groups (Ephemeroptera: Hearnden and Pearson 1991) and communities (Egglisshaw 1964, 1969, Arunachalam *et al.* 1991). Ingestion of litter by benthic animals was established by early work (Slack 1936, Jones 1950) yet until recently, its distribution and functions had received little attention (Macan 1961, 1962). Interest in litter and its role in the stream 'economy' began in the late 1960s (*e.g.* Kaushik and Hynes 1968, 1971). There are three main potential influences of litter on aquatic macro-invertebrates:

- Direct food resource for the 'shredder' feeding guild (*sensu* Cummins 1973, Cummins and Klug 1979).
- Indirect food resource, as a site for production (*via* micro-heterotrophs) and capture of fine particulate organic matter (FPOM).
- Physical substrate. Increasing the available surface area, especially when leaf packs accumulate; and introducing large-scale structure to fine sediment.

Egglisshaw (1964) found that the distribution of many riffle macroinvertebrates was influenced by litter abundance, and that similar results could not be obtained using artificial (rubber) leaves. Richardson (1992) also found that shredders were abundant on *Alnus* leaf

packs but absent on artificial (polyester cloth) packs. Differences in litter breakdown rates in fine and coarse mesh bags were attributed to shredders by Rounick and Winterbourn (1983), although shredders are not always important to litter processing (Matthews and Kowalczewski 1969, Reice 1978), especially in its later stages (Kaushik and Hynes 1971). Gut analyses have confirmed coarse detritus as a frequently important dietary item of benthic species (Minshall 1967, Coffman *et al.* 1971). There is also indirect evidence for the importance of litter as a food resource: *Gammarus pulex* became food-limited in the summer months in a Cotswold stream, ending with the leaf fall (Gee 1988).

The abundance of collectors in leaf packs was related to FPOM by Short *et al.* (1980); and differences in non-shredder abundance between natural and artificial leaves were accounted for by variation of trapped FPOM (Richardson and Neill 1991, Richardson 1992). The fine matter created *in situ* by processing of leaf litter may be of higher food value than general stream FPOM (Ward and Cummins 1979), promoting the value of litter as a habitat for collectors. 'Conditioning' of leaves by decomposers also increases the value of litter to shredders (Cummins 1974, Bärlocher and Kendrick 1973, Webster and Benfield 1986). Leaf litter species vary in their complement of fungal and microbial decomposers. Readily-decomposed species may support the most macroinvertebrates (deciduous species more than *Pinus*: Short *et al.* 1980), while both abundance and diversity increases with the progress of conditioning (Dudgeon 1982). Mackay and Kalff (1973) found caddis (*Pycnopsyche*) fed preferentially on leaf species that decayed quickly, especially those attacked by fungi.

It is intuitively clear that litter could act as a physical habitat feature and this has been shown in still water (Street and Titmus 1982), but experimental evidence in streams is hard to obtain. Litter is the case material of many caddis larvae (*e.g.* Limnephilidae: Mackay and Kalff 1973), especially in later instars (Wallace *et al.* 1990) but the minimum tolerable availability of case material has not been studied. Absence of shredders from artificial leaf litter (Egglislaw 1964, Richardson 1992) is strong evidence for the role of litter as a food resource; but does not disprove the value of litter as a physical substrate *per se*. Without food, the animals are unlikely to be found in an otherwise favourable environment.

Rounick and Winterbourn (1983) suggested that the retention of leaf litter was important in New Zealand streams, where poor shredder communities could be found despite input of litter. Riffles and backwaters were more efficient than pools and chutes in litter retention in South African streams, and supported highest shredder densities (Prochazka *et al.* 1991). Speaker *et al.* (1984) noted that accumulation in riffles (by cobbles and debris) is more permanent than accumulation in pools, due to scouring of pools during floods. Coarse woody debris is another important focus for litter retention (Bilby and Likens 1980, Speaker *et al.* 1984), especially in smaller streams. Bilby (1981) found removal of debris dams from a second-order stream produced a five-fold increase in the export of organic matter. The flexibility of leaves affects their retention by debris and coarse bed-material (Young *et al.* 1978), compounding the inter-specific differences in litter food value (Herbst 1980, Dudgeon 1982). Leaves entering the stream before senescence may require prolonged retention: Stout *et al.* (1985) found a 26-day lag between immersion and breakdown of fresh *Alnus* leaves, which are otherwise most quickly processed (Sedell *et al.* 1975, Anderson and Grafius 1975). The leaf-fall of deciduous trees is often followed by winter floods; and in coastal (or otherwise short) streams, the brief retention time may not permit leaf processing (Malicky 1990). Buried leaves may be a temporary store of organic matter because of their slower decomposition (Herbst 1980); they may also store nutrients during winter, as shown in marshes (Brinson 1977, Morris and Lajtha 1986).

Macrophytes provide an additional, instream source of organic matter (Westlake 1975, Fisher and Carpenter 1976) which can function similarly to allochthonous litter. Macrophyte 'litter' is rapidly decomposed and in unshaded streams (thus complementary to riparian sources) can contribute a large proportion of productivity (Anderson and Sedell 1979). There

has been comparatively little research on the role of senescent macrophytes, even though they may be the major source of litter in streams with managed corridors.

The River Continuum Concept (RCC: Vannote *et al.* 1980, Cushing *et al.* 1983) proposes that the proportion of shredders should be related to input of litter, and hence to canopy closure. This relationship has been confirmed in a variety of situations (above, and see review by Anderson and Sedell 1979), subject to exceptions (*e.g.* Malicky 1990) and the importance of litter retention (Winterbourn *et al.* 1981, Rounick and Winterbourn 1983, Cummins *et al.* 1984). Downstream, processing of the coarse material, reduction of canopy closure, and an increase in the importance of autochthonous production should shift the emphasis from shredders to other feeding guilds such as filterers (Minshall *et al.* 1983). In a world-wide context, extensive modifications to the RCC have been required (Cummins *et al.* 1984, Minshall *et al.* 1985, Statzner and Higler 1985), especially in prediction of longitudinal change (Ryder and Scott 1988), to recognize exceptions and removal from the pristine state. Connors and Naiman (1984) observed a trend from allochthonous to autochthonous carbon supply in first- to sixth-order streams, but emphasized the occurrence and importance of site-dependency for even pristine streams. The RCC rightly acts as a conceptual basis for investigation and discussion of processes: it cannot be applied as dogma on contemporary, modified streams.

Cultural modification of river corridors has weakened the terrestrial-aquatic linkage of most streams in Britain, although even in intensive farmland the first- and second-order streams may be wooded due to adjacent relief. Leicestershire streams still accord with the longitudinal terms of the RCC, but 'in miniature' (Harper, D.M. unpublished data). The role of litter is then expected to be greater in the upper reaches of such streams; and the features involved in litter retention (*e.g.* coarse bed material and wood debris) are consequently also important.

3.2.6 Woody debris

Coarse woody debris (henceforth 'debris') played a major role in the geomorphology of pristine streams (Sedell and Froggatt 1984, Triska 1984). Debris is generally less abundant and more localized in large than in small streams (Keller and Swanson 1979, Wallace and Benke 1984; *cf* Keller and Tally 1979, Robison and Beschta 1990) but rivers larger than any in Britain were structured on the scale of 100 km / 100 years by accumulation and breakup or debris dams (Triska 1984). The first and most consistent steps in historical river management have been removal of debris and riparian deforestation. The full realization of debris-driven processes is now limited to smaller streams in old-growth forests (Grier and Logan 1977, Robison and Beschta 1990), but stream hydrology and geomorphology can be influenced by debris of lesser abundance (Gregory 1992). The hydrograph is smoothed for light and moderate flood events in the presence of debris dams (Gregory *et al.* 1985). Accumulations of debris may be a cause of local scour but Gregory (1992) found that removal of debris increased overall sediment transport and erosion. The conditions for destructive debris flows (Benda 1990) do not generally exist in British rivers.

Debris has received considerable attention as an ecological channel feature, especially in North America, where most of the information was obtained for an extensive review by Harmon *et al.* (1986). Benke *et al.* (1984) showed that macroinvertebrate biomass and production were higher on debris (snags) than in benthic habitats, for a south-eastern USA river. Many of the invertebrate species studied by O'Connor (1991) in an Australian stream were restricted to debris samples. Some species, usually Diptera larvae, exploit debris directly as borers (Dudley and Anderson 1982, 1987, Anderson *et al.* 1984). Accumulations of debris influence retention of leaf litter (Speaker *et al.* 1984) which is an important food and habitat resource for benthic invertebrates (Egglisshaw 1964, Cummins *et al.* 1973, Prochazka *et al.* 1991). Bass (1986) found that species richness of Chironomidae, though not abundance, was higher on debris or leaf litter than on the underlying sand.

Prevalence of land drainage and flood defence objectives in channel management has led to the routine removal of debris and its sources from river corridors in Britain. Maintenance procedures, even as part of a restoration strategy (Brookes 1990), continue to specify removal of debris without provision for its role as a habitat feature. The main benefits and problems of debris, set against the requirements of conservation and flood defence, can be summarized thus:

- Reduced erosion and sediment transport.
- Physical substrate (sometimes a direct food resource) for stream invertebrates.
- Retention and proper processing of leaf litter / detritus.
- Unpredictable element of channel roughness.
- Physical hazard when mobile during floods.
- Accumulations leading to impoundment and preventing navigation.

The impact of problems associated with woody debris clearly varies with the use of the river and adjacent land. The timescale of debris accumulation, movement and dispersal in streams of moderate size is several years (Gregory *et al.* 1985, Lienkaemper and Swanson 1987). Conservative management of debris should be possible, and may be needed, as a part of channel maintenance – especially where input is enhanced by the re-vegetation of riparian areas.

3.2.7 Tree roots / undercut banks

Riparian trees (e.g. *Salix*, *Alnus*, *Acer*) or dense growth of other vegetation (e.g. *Phalaris*, *Carex*) can produce a matrix of exposed roots, especially where the toe of the bank is scoured. Rhodes and Hubert (1991) did not find qualitative differences in the fauna between undercut banks and mid-stream habitats, but the former supported a five-fold greater abundance. Others have shown tree roots to be an important habitat for specialized species, such as some Trichoptera (Jenkins and Cooke 1978, Wallace *et al.* 1990) and Ephemeroptera (Jenkins 1975). Jenkins *et al.* (1984) suggested that some apparently rare species may be more common, but unsampled, among tree roots.

Cover provided by undercut banks has been shown to positively influence trout abundance (Bowlby and Roff 1986, and see review by Wesche 1985). Boussu (1954) obtained a three-fold increase in trout biomass by enhancement of available cover. The deep pools often associated with eroded tree-root sites are also important refuges from winter flows (Côté 1970: cited by Burgess 1985). The spawning requirements of coarse fish are generally less well documented than those of salmonids. Wheeler (1978) described several species as vegetation-spawners, of which at least the roach (*Rutilus rutilus*) will use tree roots in preference to emergent or floating-leaved macrophytes (Smith, personal observation).

3.2.8 Exposed rock

Pools with a bedrock substrate support few individuals of few macroinvertebrate species (Logan and Brooker 1983, Brown and Brussock 1991). Boulders or bare rock in flowing water, however, provide an important habitat for filter-feeding species (Freeman and Wallace 1984, Huryn and Wallace 1988). Smith-Cuffney and Wallace (1987) found that production of *Parapsyche cardis* was higher on bare rock than in pebble riffles, with drift items in the range of caddis catchnets 4-10 times as abundant on the bare rock.

Boulders increase the surface area available for epibenthic species, especially if the surface of the rock is pitted. Chironomids such as *Corynoneura* and *Thienemanniella* are often found in rock fissures (Cranston 1982, Cranston *et al.* 1983). Smith *et al.* (1991) found *Austropotamobius pallipes* only amongst rocks in a pool, on the River Welland.

Thin films of water on bare rock (e.g. seepages and beside waterfalls) are a specialized habitat of smaller macroinvertebrates, the 'hygropetric zone' (Vaillant 1953, 1954). Harpacticoid and cyclopoid copepods (Gurney 1932, 1933, Harding and Smith 1960), psychomyiid caddis larvae (Alderson 1969, Jenkins 1977) and Diptera larvae such as Thaumaleidae (Smith 1989) and Chironomidae (Cranston 1984) are typical inhabitants.

3.2.9 Unclassified habitat features

There are some combinations of habitat conditions which are important in specific situations but cannot be classified according to a general list of channel features, such as downstream effects of impoundment, or coincidence with terrestrial habitats.

Lakes and reservoirs often provide an abundance of fine particulate organic matter at their outlets, which is reflected in high secondary production (Wotton 1988). There are a number of species associated with lake outlets, such as *Neureclipsis bimaculata* (Sweden: Malmqvist and Brönmark 1984, Brönmark and Malmqvist 1984), *Amphipscyche meridiana* (Java: Boon 1984) and *Simulium noelleri* (England: Wotton 1982, 1987).

Many species utilize separate habitats for life-stages, some including quite specific terrestrial requirements – the water-lily beetle *Galerucella nymphaeae* develops entirely on the upper surface of water-lily leaves, but the adult overwinters under the bark or litter of pine trees (Kouki 1991). Some damselflies select only emergent macrophytes adjacent to fast-flowing water as sites for oviposition (Gibbons and Pain 1992).

3.2.10 Habitat list

A preliminary list of in-stream functional habitats is given (Table 3.13) based upon the discussions above.

Table 3.13 Preliminary list of in-stream functional habitats

Habitat	Notes
Cobbles (more than 64 mm Ø)	Dominant substratum in some high-energy streams, or elsewhere in riffles
Gravel	Dominance with above, and where cobbles have been removed (lowland)
Sand (less than 2 mm Ø)	Point bars, patches in riffle-pool transition, or dominant in some streams
Silt	Deposited in pools, slacks, margins or off main channel
Macrophytes – Emergent	Significant aerial portion, e.g. <i>Sparganium</i> (usually grasses, rushes, reeds)
– Floating-leaved	Leaves lying on water surface, e.g. <i>Nuphar</i> and some <i>Potamogeton</i> species
– Submerged, broad-leaved	Include strap-like leaves of e.g. <i>Butomus</i> and <i>Sparganium emersum</i>
– Submerged, fine-leaved	Include fine leaves (e.g. <i>Zannichellia</i>) or dissected leaves (e.g. <i>Ranunculus</i>)
– Mosses	Aquatic types, e.g. <i>Fontinalis</i> , <i>Rhynchostegium</i>
– Macroalgae	'Cott', usually <i>Cladophora</i> and <i>Enteromorpha</i> on lowland rivers
– Marginal plants	Rooted around (e.g. <i>Phalaris</i>) or below (e.g. <i>Rorippa</i>) normal water level
Leaf litter	Deposited in pools, slacks, margins or as 'leaf packs' in riffles
Woody debris	Fallen trees, logs, substantial branches and driftwood
Tree roots	Fine exposed roots or the fibrous clumps of e.g. <i>Alnus</i> , <i>Salix</i> , <i>Acer</i>
Exposed rock	Used instream by some filterers; and in wet places (hygropetric zone)

4. FISH

4.1 Background

There are 55 freshwater fish species in Britain: none of these are endemic and three are vagrants (Maitland and Lyle 1991). More than 20 species are known to have been introduced into Britain but only 13 have established successful populations (Maitland and Lyle 1991). Most waters are capable of supporting some fish, with the exception of:

- Acidic waters (e.g. peat pools)
- Grossly polluted waters.
- High altitude reaches.
- Ephemeral waters.

The British indigenous fish can be classified thus:

1. Migratory fish with a marine propensity (which are hence euryhaline)
2. Fish with a dispersal mechanism which has taken them far beyond their original catchment.
3. Fish with a poor dispersal mechanism which are hence confined close to their original catchments.

In general, in the North Temperate zone, the number of fish species increases southwards. Hence in Britain, many species are confined to the south and east, whilst few are limited to the north and west (Maitland and Lyle 1991):

Wide distribution (all found in both lentic and lotic situations) –

Salmon, trout, pike, minnow, roach, eel, three-spined stickleback, perch.

Mainly southern distribution –

Generally lentic: crucian carp, tench, bream, silver bream, rudd, chub.

Generally lotic: sea lamprey, river lamprey, brook lamprey, grayling, gudgeon, bleak, dace, stone loach, ruffe, bullhead, flounder.

4.2 Trout (*Salmo trutta* and *Oncorhynchus mykiss*)

4.2.1 Habitat summary

- Distribution See map (Figure 4.1)

Spawning

- Water depth Moderate (mean 32 cm)
- Substratum Gravel, avoids silt (mean 14 mm)
- Flow rate Fast, avoids velocity $< 12 \text{ cm s}^{-1}$ (mean 39 cm s^{-1})
- Flow source Prefers groundwater seepage.

Fry and adults

- Water depth Fry – shallow (5-7.5 cm)
Adults – deeper (> 20 cm)
- River width Narrow.
- Substratum Coarse (size range 50-70 mm)
- Flow rate Minimum velocity 15-20 cm s⁻¹
- Flow type Riffle-pool sequence.
- Temperature Maximum 24 °C
- Aquatic vegetation Rooted plants, weed beds, such as water buttercup (*Ranunculus* spp.), water speedwell (*Veronica* spp.) and watercress (*Rorippa* spp.)
- Terrestrial vegetation Minimum 6 m vegetated buffer zone recommended.
- Shelter Undercut banks, submerged logs, rocks, submerged and overhanging vegetation.

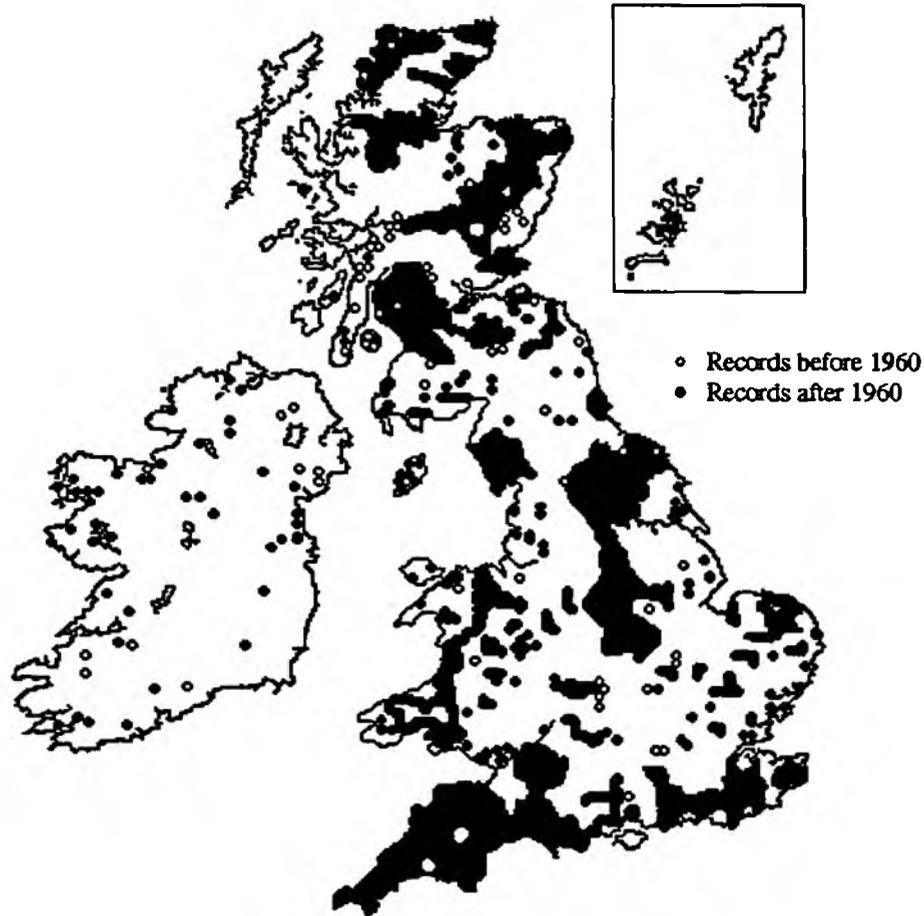


Figure 4.1 Broad distribution of the brown trout in the British Isles (Maitland 1972)

4.2.2 Introduction

Two species of trout are found in British waters: the brown trout (*Salmo trutta*) and the rainbow trout (*Oncorhynchus mykiss* = *Salmo gairdneri*). The rainbow trout is indigenous to certain tributaries of the Sacramento River in North America and was first introduced to Europe in 1882 (Frost and Brown 1967). The rainbow trout is very similar in appearance to the brown trout but can be distinguished by the presence of spots on the caudal fin and iridescent bands on the side of its body. The brown trout is indigenous in Europe, north Africa and west Asia. The habitat requirements of trout can be divided into four elements: water, space, shelter and food. The availability of suitable habitats may vary seasonally within rivers and the requirements may also vary according to different life stages and activities.

4.2.3 General character of trout streams

Many rapidly flowing narrow streams rising on hard rocks, characteristic of north and west England, west Scotland and Ireland, provide extensive suitable spawning grounds for trout (Frost and Brown 1967). Trout are less common in areas where pike, perch and cyprinids (e.g. rudd, roach, dace and chub) predominate. The difference in distribution between brown trout and coarse fish may solely be due to physical differences; but biological factors of competition and predation could also contribute (Frost and Brown 1967).

4.2.4 Life history

Brown trout spawn in running water between October and February, and they have specific requirements for spawning (see Section 4.2.5). Female brown trout excavate holes in the gravel into which they deposit their eggs – these areas are called 'redds'. Spawning places are usually of moderate depth and velocity (though not in turbulent riffles); such conditions are usually found at the tail of a pool or at the edge of a river. Between January and March 'alevin' hatch from the eggs, and when the yolk supply is exhausted they move towards the light and face the current – the alevin then feed on benthic and drifting invertebrates.

When the alevin reach 3.2 cm length they are referred to as 'fry'. Fry tend to inhabit shallow mid-water areas (5-7.5 cm depth) maintaining their position against the current. They hold linear territories of about 7.5 cm, with larger fry probably holding more desirable territories (e.g. better food availability). At the end of their first year, the fry have grown to 5-14 cm.

Second year fish are referred to as 'yearlings'. They tend to occupy the same areas as larger and older fish (Frost and Brown 1967). The primary food source of trout shifts from insects to fish when they have grown to about 35-40 cm (Clapp *et al.* 1990).

4.2.5 Spawning

White and Brynildson (1967) list the following as having an important influence on the natural reproduction of trout:

- Temperature.
- The size and texture of substrata.
- Stream discharge.
- Stream gradient.

In a study on microhabitat preferences for spawning, Shirvell and Dungey (1983) found that substratum size, water depth and velocity were relatively constant spawning parameters.

Brown trout preferred a mean depth of 31.7 cm, a mean velocity of 39.4 cm s⁻¹ and a mean substratum size of 14.0 mm for spawning. Substratum size seems to be the most important factor determining choice of spawning sites, but is in turn determined partly by water velocity. High water velocity is important for sediment sorting and also the irrigation of developing embryos. Brown trout choose positions with optimum combinations of several variables rather than selecting for any single factor (Shirvell and Dungey 1983). Grost and Hubert (1990) carried out a study to quantitatively describe the surface features of brown trout redds constructed by a resident population of brown trout in Wyoming. The results were compared with those of Reiser and Wesche (1977: before an increase in the minimum flow level). Water depth was found to be unchanged, most frequently 12.3-18.3 cm; but the depth range used for spawning became narrower and shifted slightly towards deeper water following the flow increase. Grost and Hubert found that the mean water velocity at the front of the redd was 34 cm s⁻¹ and similar values were recorded by Ottaway *et al.* (1981). Brown trout avoid water velocity below 12 cms⁻¹ during spawning (Grost and Hubert 1990); and it has been suggested that salmonids, regardless of their size, have a minimum velocity requirement of 15-20 cm s⁻¹ during spawning (Crisp and Carling 1989).

Streams supplied by ground water are often selected for spawning by brown trout (*Salmo trutta*), brook trout (*Salvelinus fontinalis*) and probably other salmonids (Jones 1959). Spring-fed streams provide a constant flow over the eggs, maintaining sufficient dissolved oxygen; and also, since ground-water temperatures are more consistent than runoff, the eggs are protected from cooling and delayed hatching.

4.2.6 Diet

The diet of trout varies in quantity and quality between locations, seasons and times of the day (Frost and Brown 1967). The trout is essentially an opportunist carnivore, consuming a variety of invertebrates, including insects, molluscs and crustaceans. The Community Fisheries Involvement Program (Anon. 1980) report that trout below 30 cm length feed primarily on invertebrates (both aquatic and terrestrial) including mayflies, stoneflies, caddisflies, crayfish, midges, beetles, grasshoppers and dragonflies. Relative abundance and ease of capture seem to be the two criteria that determine which food source predominates. Table 4.1 (from Kelly-Quinn and Bracken 1990) shows the variety and abundance of organisms in the diet of brown trout; those less than one year old mainly consume aquatic organisms. In June to September, mayfly nymphs and chironomid larvae were recorded as the main food source, whilst in late autumn and winter the proportion of *Gammarus duebeni* in the diet increased. The diet of older trout includes prey items that were unimportant during early development, taking a greater percentage of adult invertebrates; and in winter crustaceans.

The proportions of different taxa in the diet of brown trout was found to vary significantly between sites. This is most likely related to different abundances of prey due to differences in geology and water chemistry. Kelly-Quinn and Bracken (1990) highlighted seasonal changes in the diet of trout. Adult insects were the most important during the early spring and summer months when they constituted 51% of the biomass of food consumed by fish over 2 years old.

Riffles are the most important food producing areas within streams as they provide well-oxygenated water, shelter, space and food for prey (Frost and Brown 1967). The coarse substratum in riffles traps leaf litter which provides a major source of food for invertebrates.

Table 4.1 Taxa recorded in the diet of brown trout (Kelly-Quinn and Bracken 1990)

Taxon	Freq.	Taxon	Freq.
Nematoda		Coleoptera	
spp. indet.	•	<i>Haliphus</i> sp.	A•
Oligochaeta		<i>Hyphydrus</i> sp.	A•
<i>Lumbriculus variegatus</i>	•	<i>Hydroporus</i> sp.	L•
<i>Nais elinguis</i>	•	<i>Oreodytes</i> sp.	L•
Hirudinea		<i>Deronectes</i> sp.	L•
<i>Erpobdella octoculata</i>	•	<i>Dytiscus</i> sp.	L•
Isopoda		<i>Hydraena riparia</i>	A••
<i>Asellus aquaticus</i>	•	<i>Helophorus</i> sp.	L• A•
<i>Gammarus duebeni</i>	•	Trichoptera	
Ephemeroptera		<i>Rhyacophila dorsalis</i>	L••• A•
<i>Baetis muticus</i>	L•	<i>Rhyacophila munda</i>	L•
<i>Baetis rhodani</i>	L•••	<i>Glossosoma</i> sp.	L•
<i>Rhytrogena semicolorata</i>	L•••	<i>Agapetus delicatulus</i>	L••
<i>Ectyonurus dispar</i>	L•• E• A•	<i>Agapetus fuscipes</i>	L••• A•
<i>Ephemerella ignita</i>	L•	<i>Hydroptila</i> sp.	L•
Plecoptera		<i>Agraylea</i> sp.	L•
<i>Brachyptera risi</i>	L•	<i>Philopotamus montanus</i>	L•
<i>Amphinemura sulcicollis</i>	L•••	<i>Wormaldia</i> sp.	L•
<i>Protonemura meyeri</i>	L•••	<i>Hydropsyche instabilis</i>	L••• A•
<i>Protonemura praecox</i>	A•	<i>Polycentropus flavomaculatus</i>	L•
<i>Leuctra fusca</i>	L••	<i>Drusus annulatus</i>	L•
<i>Leuctra hippopus</i>	L•••	<i>Limnephilus</i> sp.	L•
<i>Leuctra inermis</i>	L••	<i>Potamophylax</i> spp.	L•
<i>Leuctra</i> spp.	L•	<i>Silo pallipes</i>	L•
<i>Isoperla grammatica</i>	L••	<i>Sericostoma personatum</i>	L•
<i>Chloroperla torrentium</i>	L•	<i>Odontocerum albicorne</i>	L•
<i>Chloroperla tripunctata</i>	L••	Tipulidae	
Heteroptera		<i>Tipula</i> sp.	L•
<i>Velia</i> sp.	A•		

Frequency symbols: L larvae or nymphs, E exuviae, A adults, • rare, •• common, ••• dominant

4.2.7 Flow and geomorphology

The flow in a river is heterogenous and may be classified thus:

1. Cascades. These areas provide very few 'lies' for trout. Lies are areas of reduced flow where trout do not have to constantly battle against the current.
2. Riffles. These areas provide little shelter from the current but many smaller trout are resident, with larger fish coming in at dusk due to local food abundance (Frost and Brown 1967). To the age of one year, trout live along riffle margins where rocks, woody debris and plant material offer concealment (Anon. 1980).
3. Flats. Due to the associated silt, spawning areas are limited and feeding is poorer. Weeds provide habitat for some food organisms and may also provide shelter (Frost and Brown 1967).
4. Pools. Spawning areas and food organisms tend to be scarce in pools, but they are good areas of shelter. Coarse fish are frequently found in pools.

The topography of an area is of great importance as it can determine the various elements that form a stream's character. The underlying geology influences the suitability of areas for trout by affecting the water quality and quantity, current speed, substratum, associated flora and fauna and also the availability of shelter. Within a trout stream, fish are more numerous

where the bottom is eroding than where it is depositing. Trout only spawn successfully on eroding substrata and this is therefore a primary requirement for the natural maintenance of a stock (Frost and Brown 1967). Trout have very specific sets of requirements at different stages of their life cycle and for different activities. If the space these fish require is not present, the development of populations will be interrupted (Anon. 1980).

The margins of riffles provide easy access to the food-rich main riffle. As the trout grow, they move to swifter flowing areas where they hence require structures to break the current. When older than one year trout occupy deeper water which provide more protection from predators, such areas are frequently found in runs and at the heads of pools (Anon. 1980).

Heggenes (1988) studied the substratum size preferred by different sized under-yearling brown trout in artificial stream channels. It is difficult to evaluate the importance of water velocity and substratum separately as water velocity in part determines substratum character. Heggenes found that brown trout fry (independent of fry size) showed a strong preference for coarser substrata (50-70 mm) compared with other gravel sizes offered. Coarser substrata provide better cover in the interstitial spaces, and may also provide increased visual isolation from other fry competing for space. However, coarse substrata only provide cover when interstitial spaces are free from silt.

The temperature of the water also influences the use of the substratum as refuge. Heggenes (1988) found that fry hid significantly more in the substratum at low temperatures than at high temperatures. Cunjak and Power (1986) suggested that low temperatures trigger a daytime winter hiding response in areas of coarse substratum. Light levels also significantly influence the substratum preferences of brown trout fry. Fry were observed moving over the substratum in the dark, leading Heggenes to conclude that darkness also functioned as cover.

The stream gradient affects current speeds which consequently influence the substratum type. Current speed can have a direct effect on the growth of trout, as in areas with high flow rates more energy is expended in maintaining a constant position.

4.2.8 Water quality

Aspects of water quality that affect trout distribution are temperature, turbidity, nutrient enrichment and the presence of chemical toxins.

Rainbow trout and brown trout can tolerate a maximum temperature of 24 °C (Anon. 1980). The shade from bank vegetation has an important role in preventing waters becoming too warm. However, too much shading can result in a decrease in the growth of plants upon which the invertebrate food of trout rely, leading to a decrease in the food supply for trout. The optimum percentage of shading to balance cool water temperatures and optimum food production varies between streams; depending on the proportion of cooler groundwater, stream width and valley development (Anon. 1980).

Fish metabolic rate increases with temperature. Elliott (1973) found that temperature influenced the required frequency of meals and also the capacity of the stomach; higher temperatures lead to an increased stomach capacity and an increased rate of gastric evacuation. The energy requirements for metabolism are increased with temperature and with body weight. These factors together determined the amount of energy left for growth, but the time of feeding was determined by availability of food organisms in the drift.

Catchment land use can have profound effects on the quality of river water. The removal of bank vegetation and intensive farming practices can lead to increased particulate and dissolved loading (e.g. from silt, manure, pesticides and fertilisers). A minimum vegetated

riparian zone of 6 m was suggested by the Community Fisheries Involvement Program (Anon. 1980) – this retards runoff, decreasing the proportion of material entering the stream.

A study on the ecological effects of low flows on chalk streams by Wiltshire Trust for Nature Conservation (Giles *et al.* 1991) identified negative effects on trout stocks due to siltation. The deposition of silt on the gravel spawning areas in January and March can lead to reduced egg and alevin survival. Young trout are also adversely affected by reduction of hydraulic roughness due to silting, and the loss of plant cover which otherwise provides shelter from flow, predators and aggressive behaviours.

Nutrient enrichment can result from a number of sources such as waste water input, agricultural and urban runoff. Enrichment leads to an increase in algal growth which can physically block the river and cause de-oxygenation.

4.2.9 Water quantity

The quantity of water in trout streams and rivers is important, as it has complex interactions with many other environmental factors (temperature, dissolved oxygen, sedimentation, vegetation growth and food availability). Recently there has been increasing concern about the consequences of low flow rates in British chalk streams (Giles *et al.* 1991). The prolonged low flows which are a result of abstraction are threatening salmonid stocks: either directly due to drying out of streams; or indirectly due to the reduction in the area of riffles and accelerated sedimentation.

Flow regimes affect algal and plant growth. The development of algae such as *Cladophora* limits the development of *Ranunculus* which is of importance for many of the invertebrates which make up a high percentage of the trout's diet. Siltation blocks interstitial spaces in the substratum hence reducing the numbers of insect larvae. The invertebrate community shows a shift in dominance patterns with the importance of Crustacea and predators increasing, and prevalence of tube-dwelling invertebrates such as *Tubifex* spp. and some Chironomidae.

Flow reduction limits the growth of submerged macrophytes (e.g. *Ranunculus*) and favours the growth of invasive marginal plants such as *Rorippa nasturtium-aquaticum*. The mosaic pattern of weed beds and gravel patches typical of a summer chalk stream, is replaced by silted reaches interspersed with large areas of *Rorippa* etc. Finally, low flows can also lead to a build up of organic material, resulting in eutrophication and de-oxygenation.

4.2.10 Cover

Trout often live adjacent to turbulent areas because they feed on the invertebrate drift brought to them on the swift currents (Frost and Brown 1967). They ideally like to be protected on three sides by their shelter, occupying less demanding flow conditions whilst gaining protection from predators (White and Brynildson 1967). Fry take shelter along the shallow, slow margins of streams, but more substantial cover is required by larger fish e.g. deep or turbulent water, undercut banks, woody debris, submerged or overhanging vegetation, rocks and other objects (broken water also provides concealment). Beds of aquatic plants such as *Ranunculus*, *Veronica* and *Rorippa* may provide cover for young and adults.

Wesche (1976) found that the standing crop of brown trout in a Wyoming stream was strongly correlated with the availability of cover. Lewis (1969) suggested that water velocity and cover not only influence position but are the primary features regulating brown trout population density in streams. DeVore and White (1978) found that 25-30 cm brown trout

responded better to cover that was located close to the bed of the stream; it was suggested that the primary response was negative phototaxis because trout were not observed to use tactical stimuli and there was no measurable change in flow rate.

Boussu (1954) showed that loss of brush and undercut banks from sections of a stream (i.e. a decrease in available cover) produced a decrease in trout biomass and population density. Adding brush cover subsequently increased the weight and number of trout. Aquatic vegetation was also noted to be of value, both when rooted and after becoming detached. Rooted plants tended to be utilised as cover for smaller fish, whilst floating matter was utilised by fish of all sizes. White and Brynildson (1967) noted, however, that excessive floating vegetation (and other debris) can accumulate silt in low-gradient reaches, possibly covering spawning sites and the food-producing surfaces of rocks and vegetation.

Emergent plants, and overhanging riparian vegetation, can provide cover for trout at the waters edge. To preserve and improve such a habitat, it must be protected from shade and grazing – if not fenced, grazing animals will eat plants and trample overhangs, leading to bank failure.

In Wisconsin, broad-leaved annuals mixed with grasses (in particular *Phalaris arundinacea*) were best for bank soil stabilization and provision of overhanging cover (White and Brynildson 1967). The root systems of *Salix* are also noted as effective bank stabilizers, whilst allowing the formation of undercuts and hollows. However, unmanaged mature willows with dense canopies restrict the growth of both instream vegetation and further willow saplings. Coppicing has been recommended for maintenance of stands of willows along waterways. Branches of *Alnus* draping into the water can also provide trout cover, but may provide too much shade over small channels.

North American studies have shown that artificial cover can lead to an increase in the number and size of trout in a given areas (Tarzwell 1937). Structures which provide direct cover can be placed in streams in order to increase productivity. These can be fixed or floating objects placed adjacent to the river bank to simulate the missing vegetation cover (Welcomme 1985). White and Brynildson (1967) suggested that structures should be placed on the outside of bends in order to provide ideal hiding places for trout. Submerged objects such as logs, boulders and branches also provide cover (Welcomme 1985).

4.2.11 Biotic interactions

Competitive interactions can occur between trout or with other species. Shirvell and Dungey (1983) were uncertain whether brown trout occupy particular positions from preference or obligation. Competitive interactions may limit the availability of preferred habitat as competition forces individuals into sub-optimal areas. However, Jenkins (1969) found that when competitors were removed from a stretch of river, individuals occupied the same positions, suggesting that competition did not influence positional choice.

Kennedy and Strange (1982) found significant differences in habitat selection between different age classes of brown trout, with older fish moving to deeper areas. They observed 72.2% of fry, but only 7.4% of adult fish, in water less than 20 cm deep. Everest and Chapman (1972) found similar age-specific partitioning amongst chinook salmon and rainbow trout. This move to deeper water may merely be due to the physical dimensions of the larger fish or it may be due to the increasing competitive success of larger fish (Jenkins 1969). Deeper water might be colonised by a greater number of fry in the absence of competition and predation from older conspecifics. It is unlikely that depth alone is the major limiting factor in any habitat choice, but such behaviour would reduce inter-cohort competition (Kennedy and Strange 1982).

Competition for food varies with the size and age of trout, with the seasons and in different types of water (Frost and Brown 1967). Jenkins (1969) found that – independent of age or size – adults of both rainbow trout and brown trout were aggressive when feeding on drift. There was a stable hierarchy decided by size, sex, age and previous experience; with occupation of sub-optimal lies by lower-ranked fish. Jenkins (1969) hypothesized that resident trout form fairly stable social structures centred around desirable areas; with the number and size of groups being a function of population density combined with the distribution of suitable lies.

The relationship between trout and other species of fish living in the same body of water depends on the degree to which their fundamental needs coincide. Where young trout and salmon are found, competition can occur. Since young trout are more aggressive than young salmon they can drive salmon away from better territories. However, young trout show a greater preference for winged insects than young salmon, reducing competition for food when food is sufficiently abundant and varied. There is little information on interspecific competition involving trout in running waters. Small species such as minnow, bullhead, loach, gudgeon, stickleback and eel may be numerous and competition with young trout presumably happens; as between adult trout and coarse fish such as chub, rudd, dace and bream which overlap in their diet (Frost and Brown 1967). No competition for breeding spaces occurs because trout spawn at a different time of year, on different substrata to coarse fish species. Predation by pike, preferring medium-sized trout, affects the population structure as well as its total number. Eels have been considered by some to be a major predator of trout but Frost and Brown (1967) found no evidence for this from examination of eel stomach contents.

4.3 Salmon (*Salmo salar*)

4.3.1 Habitat summary

- Distribution See map (Figure 4.2)

Spawning

- Water depth At least 1 m
- Substratum Gravel, avoid siltation.
- Gradient Low.
- Flow type Run-pool sequence.
- pH ≥ 4.5 (optimally circumneutral)
- Chemistry $[O_2]$ 5-7 mg l⁻¹

Fry and adults

- Water depth 15-45 cm
- Substratum Gravel.
- Flow rate 15-35 cm s⁻¹
- Flow type Riffles (feeding)
- Pollution Sensitive; also require low turbidity.

- Temperature
- Cover

Tolerance 0-25.3 °C, maximum growth 7-19 °C
 Overhead: undercut banks, overhanging vegetation.
 Submerged: aquatic plants, logs, boulders.

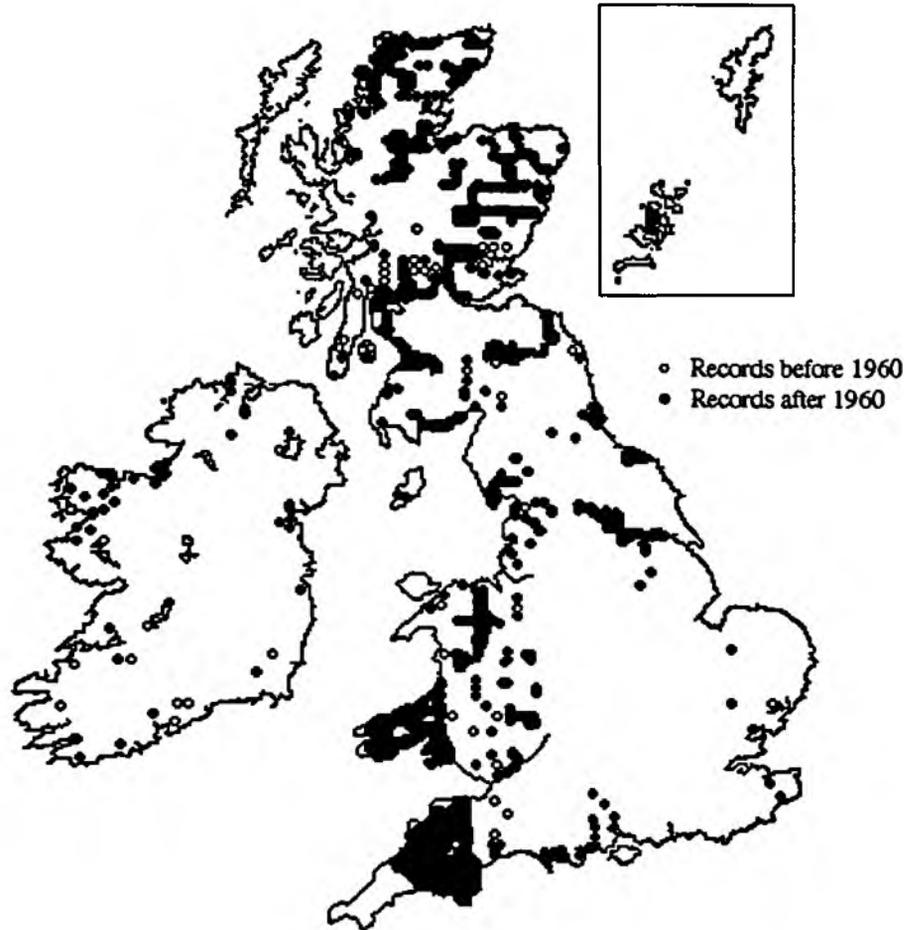


Figure 4.2 Broad distribution of the salmon in the British Isles (Maitland 1972)

4.3.2 Life history

The adult salmon enters the river to breed in the autumn or early winter. The female selects a riffle area with a gravel or cobble substratum and makes a 'redd' (20 cm depression in the gravel: Thomas 1962). The eggs are fertilized in the redd and covered with more gravel; many spawned adults or 'kelts' die but the survivors return to the sea and may breed again. The young remain in the gravel whilst their yolk sacs are intact (alevins), emerging after about 100 days as feeding 'fry' or 'fingerlings'. When the fry have reached a length of 4-6 cm they develop vertical stripes, or 'parr marks'. It is only after 3 or 4 years that individuals become silvery, and (as smolts) migrate to the sea.

4.3.3 Spawning

Many rivers have areas of gravel – apparently suitable for redds – which are never utilised by salmon (Jones 1959), so their requirements are not fully understood. In limestone-

rich streams female salmonids may have problems in digging redds if marl (calcium carbonate) has encrusted the gravel. Mills (1973) studied salmon spawning areas, concluding that stream gradient was the main factor in stream accessibility for salmon, although depth, width, and mean flow were also important. Acceptable spawning ground is probably influenced strongly by fish size, with large fish being able to dislodge coarser substrata and withstand swifter currents (Keenleyside 1979).

Jones (1959) noted that an ideal spawning ground for salmon in a river is an area of gravel, at least 1 m deep, sloping gently downstream with large pools at either ends. A riffle-pool sequence in streams is important not only in providing cover, resting and food-producing areas, but also the necessary hydraulic, chemical and physical conditions for successful development of the incubating eggs. Thus, salmon select the interchange area between a riffle and a pool which is a good environment for proper development of eggs. At the riffle-pool boundary, the velocity is great enough to carry away silt and debris that may clog the redd substratum. Secondly, the movement of water into the gravel provides a constant supply of oxygen which may be the most important condition for successful incubation of the salmonid eggs, with oxygen demand increasing as the eggs develop (Bardach *et al.* 1972: cited by Mundie 1974). Siltation of the gravel during the incubation period can be fatal, as the eggs are likely to be starved of oxygen (Cooper 1980). Thompson (1974) found the required interstitial dissolved oxygen levels for the spawning salmonids to be around 5.0 mg l⁻¹ during incubation and 7.0 mg l⁻¹ for hatching. Water movement also removes metabolites.

Atlantic salmon tend to spawn in circumneutral waters (Jones 1959) and the growth of larval salmonids is retarded at pH below 4.5. Temperature is also important for incubation since higher temperatures increase the rate of egg development: e.g. brown trout eggs take 156 days to hatch at a temperature of 1.6 °C, but only 41 days to hatch at 10 °C. However, excessive temperature rises may cause problems such as increased time to fertilisation (Lindroth 1942: cited by Nall 1955) and prolonged exposure to high temperatures may be lethal.

4.3.4 Diet

Salmon of all ages are opportunistic carnivores (Carpenter 1940, Allen 1941). The fry eat drifting insects, particularly the larvae of Chironomidae, Ephemeroptera, Plecoptera, Trichoptera, and insects of terrestrial origin. Parr and smolt eat mayflies, caddisflies, snails and worms as well as other fish species: riffles are the primary feeding sites.

According to Mundie (1974) studies have shown that salmonids feed primarily on organic drift carried along with the current. This feeding occurs mainly in the mornings and evenings ceasing altogether at night. This has been attributed to the fact that salmonids feed by sight and drifting items are not visible to the fish at night. Benthic invertebrates drift most abundantly during the night, between the hours of approximately 16.00-04.00 (Chapman and Bjornn 1969). These factors suggest that much of the food present for fish is not being used by them (Kalleberg 1958). Mundie (1974) has noted that in mid- to late summer, and in times of low flow, aquatic insects are scarce, and Kalleberg (1958) reported a summertime increase in salmon chasing aerial insects.

Much of the energy to support the stream fauna comes from the land surface in the form of leaf litter, woody debris and dissolved organic matter, with some estimates of the energy input from allochthonous sources accounting for 50-99% of energy consumed in a stream ecosystem. Deforestation and bank clearance can have a great impact on the riverine ecosystem. Mills (1967) found that the standing crop of young salmonids was much higher in a stream supporting abundant vegetation, than in areas with little vegetation. Conversely, extreme canopy closure can reduce growth of aquatic plants and limit the scrub and ground-level

vegetation. Abundant leaf litter can lead to deoxygenation of the stream as a consequence of its decomposition (Smith 1980).

4.3.5 Flow and geomorphology

Stream velocity is the primary physical parameter controlling salmonid habitat selection, with a preferred range of 15-35 cm s⁻¹ (Degraaf and Bain 1986, Morantz *et al.* 1987). Water velocity governs the rate of oxygen renewal to the benthic fauna and influences invertebrate drift: thereby determining food availability (Chapman 1966, Waters 1969).

Substratum size affects the standing crop of benthic invertebrates which is greater in gravel compared to smaller substrata. Larger particles provide insects with a firm surface on which to cling whilst offering protection from the force of the water current (Jones 1959). The increased invertebrate biomass of gravel beds favours the salmon.

Like stream velocity and substratum size, water depth influences habitat selection by benthic organisms (Degraaf and Bain 1986, Morantz *et al.* 1987). The level of light attenuation within the water column is affected by depth, this in turn regulates the levels of photosynthetic production and controls the benthic standing crop. In general, the areas of highest productivity in salmonid streams have been found at depths of 15-45 cm; though these sites are only used by salmon in the presence of suitable substratum and velocity (Degraaf and Bain 1986).

4.3.6 Water quality

Much of the information relating to trout (see also Section 4.2.8) is applicable to the freshwater stages of salmon. Clear waters are preferred as suspended sediment can cause abrasive injuries to fish gills; and its deposition reduces the quality of coarser substrata for feeding or spawning.

Stream temperature is extremely important to salmonids and their food supply: variations in water temperature may be lethal. The absolute temperature tolerance of trout lies between 0-25.3 °C, although the range for maximum growth is 7-19 °C (Hynes 1970). Cold streams shaded by dense forest canopies are probably not the best conditions for salmonids (White and Brynildson 1967), even though water temperatures tend to be less variable in forested areas rather than open sections of streams (Smith 1980).

White and Brynildson (1967) suggested that streams may be favourably altered to maintain the temperature range within the range of rapid trout growth – controls must aim to reduce direct sunlight hitting the stream during the spring and summer months, whilst minimising the loss of heat by outward radiation in the winter. Extremes in water temperature can be reduced by removing obstructions to flow which may lead to impoundment. In areas of low gradient, removal of any obstructions over 15 cm will help to make water temperatures more favourable for salmonids. A certain amount of tree/bush cover is desirable to produce adequate shade so as to block out some direct sunlight. Streams and springs running into the river channel must be similarly managed – if the land around the tributaries is cleared, then the temperature of the water flowing into the river channel will be warmer, causing an increase in temperature in the main channel. Ensuring adequate shade of streams and springs is essential and may necessitate the removal of livestock from the stream edge in order to help encourage vegetation growth.

The Atlantic salmon is very sensitive to pollution, which is reflected in its distribution (Jones 1959). White and Brynildson (1967) have observed naturally infertile streams that support trout only below the point where they receive sewage from a town. Mills (1969)

attributed a large increase in fish biomass to the nutrients made available by the addition of mineral fertilisers to a stream, although these effects were short-lived. Tank experiments have proven that fish can thrive on pellets produced from recycled waste (Starbird 1972), and they have been suggested as a dietary supplement for free-living salmon. There are thus some benefits to be derived from organic enrichment of salmonid streams; but eutrophication changes the whole ecology of a river and most opinion is against its intentional encouragement.

4.3.7 Cover

The need for shelter varies daily (Chapman and Bjornn 1969) and according to body size. Suitable cover affords protection from both high current velocities and predation, and allows for more efficient hunting. It has been observed that both overhead cover (overhanging vegetation) and submerged cover (stream substratum, aquatic vegetation) are very important in all stages of salmonid life. Thus, riffle-pool streams with the appropriate gravel need to provide not only suitable spawning sites for the salmon but also cover for protection of the eggs and the newly hatched larvae.

4.3.8 Biotic interactions

Competition is likely between young of the Atlantic salmon and trout, minnows, stone loach and three-spined sticklebacks due to the similarity in their diets (Maitland 1965).

Salmon have a variety of predators. Many investigators have recorded avian predators: herons, black-headed gulls and ducks (Berry 1936), kingfisher and mergansers (White and Brynildson 1967, Elson 1962). Jones (1959) described how swans and teal poked their bills amongst the gravel where salmon had spawned. Perch (*Perca fluviatilis*), ruff (*Gymnocephalus cernua*), pike (*Esox lucius*), eels (*Anguilla anguilla*), brown trout (*Salmo trutta*) and chub (*Leuciscus cephalus*) are all common predators of salmon fry and young parr. Heggenes and Borgstrom (1988) included mink (*Mustela vison*) as a factor in salmonid abundance.

4.4 Chub (*Leuciscus cephalus*)

4.4.1 Habitat summary

• Distribution	See map (Figure 4.3).
• Altitude	Intermediate. May also be found in faster flowing upstream and lowland downstream stretches.
• Depth	Variable.
• Substratum	Gravel beds with submerged stones.
• Flow rate	Variable within channel: moderate (foraging), below 20 cm s ⁻¹ (shelter)
• Aquatic vegetation	Macrophytes for spawning, cover and feeding (on macro-invertebrates)
• Marginal vegetation	Reedbeds.
• Terrestrial vegetation	Bankside trees.
• Diet	Omnivorous: fish, plants, invertebrates.
• Water temperature	Prefer mean > 12 °C

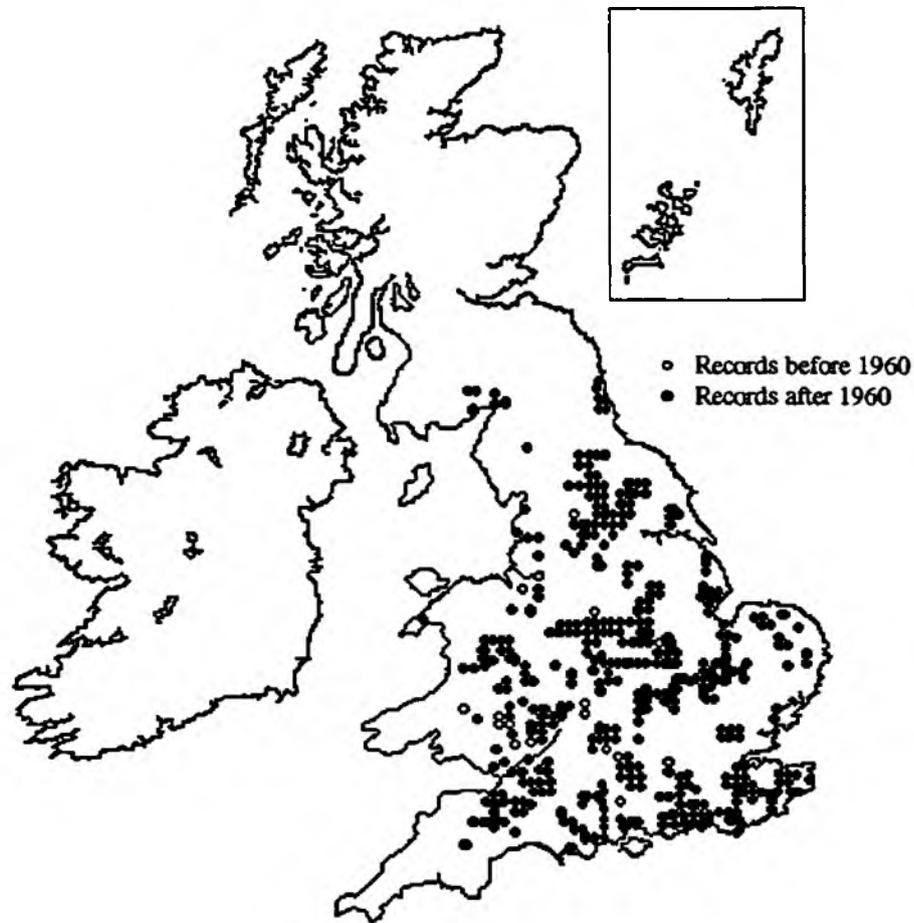


Figure 4.3 Broad distribution of the chub in the British Isles (Maitland 1972)

4.4.2 Introduction

Chub (*Leuciscus cephalus*) are generally found in the middle reaches of rivers, although able to adapt to faster flowing upstream reaches of typical trout streams and also slow-flowing lowland reaches. The dorsal scales are dark green/grey/black, whilst its sides and ventral surface are silvery-white. The chub has a life expectancy of up to 12 years. Individuals reach a length of 30-50 cm and weigh about 2.7 kg, although this varies between rivers (maximum 61 cm and 7.25 kg in continental Europe: Wheeler 1978). The chub is valued by anglers though it is poor to eat.

4.4.3 Life history and spawning

The male chub matures after 3-4 years, whilst the female cannot breed until the age of 5-6 years; but the female tends to live longer (Leeming 1963). Chub spawn in May-June choosing shallow gravel beds in which to lay their eggs (often in smaller tributaries); the yellow eggs (2 mm Ø) adhere to nearby stones and vegetation, and hatch after 8-10 days (Wheeler 1978). The sex ratio of the fry is weighted towards males (1:1.6) but this bias does not persist, due to earlier male mortality. Within limits, the rate of recruitment into the population increases with water temperature (due to the associated increase in fry growth rate). A study of the chub population of the River Stour found that average water temperatures > 12° C lead to accelerated growth rates (Mann 1976). In comparison to other coarse fish, the chub has a slow growth rate

in its first 2 years. There appears to be no cannibalism (Mann 1976), and hence a strong recruitment one year will not suppress future age classes.

4.4.4 Diet

Chub are omnivores; prey size and type generally alters with age. The diet shifts away from aquatic invertebrates (e.g. insect larvae and crustaceans) towards plant matter and fish (Wheeler 1978; and see Table 4.2). The diet of the older fish is moulded by the seasonal availability of plant matter, with the winter intake of *Cladophora* being replaced in the summer by the leaves and stems of plants such as *Potamogeton* and *Myriophyllum* (Leeming 1963).

Table 4.2 The contents of the fore-gut of chub from the River Stour (Mann 1976)

Length of fish (mm)	0-49	50-149	≥ 150
Sample size	71	59	87
% number of organisms			
Ephemeroptera nymphs	9.5	1.6	4.3
Ephemeroptera adults		4.9	
Trichoptera larvae	4.8	1.6	13.0
Aquatic Coleoptera	1.9	4.9	6.5
<i>Simulium</i> larvae	3.8	16.4	
Chironomidae larvae	38.1	4.9	8.7
Tipulidae larvae	2.9	1.6	
Aquatic Hemiptera		36.2	
<i>Austropotamobius pallipes</i>			8.8
<i>Gammarus</i>	1.9		4.3
Cladocera	7.6	21.4	
Mollusca			2.2
Pisces		1.6	34.8
Mallard (<i>Anas platyrhynchos</i>)			2.2
Other aquatic organisms	20.0		10.9
Other terrestrial organisms	9.5	4.9	4.3
% frequency of occurrence			
Macrophytes	1.4	6.8	37.5
Algae	11.3	3.4	10.7
Empty fore-gut	16.9	39.0	30.7

4.4.5 Flow and cover

At an early age the chub moves around in schools inhabiting the extreme margins of the channel in areas of minimal flow. When older it adopts a more solitary lifestyle and is often found amongst weed beds in fast, deep water. Chub forage at night, selecting refuge habitats in daylight. These refuges are formed by a combination of lower water velocity ($< 20 \text{ cm s}^{-1}$) and overhead cover: it is believed that by resting in slack water the chub minimises its energy expenditure (Smith 1989). In addition to energetic considerations, the shaded conditions of cover camouflage the fish by reducing background light, which might also enhance ability to detect both prey and predators in the adjacent body of water. In the evening, the chub positions itself in faster flows (although it does not necessarily select the fastest stretches); at such times the affinity for cover is suppressed but not removed. Hence, general features for chub habitat are bankside tree cover and variation in the flow velocity across the channel (Smith 1989).

4.5 Bream (*Abramis brama*)

4.5.1 Habitat summary

- Distribution See map (Figure 4.4)
- Altitude Lowland.
- Depth Shallow.
- Flow rate Slow.
- Aquatic vegetation Dense.
- Diet Aquatic invertebrates.

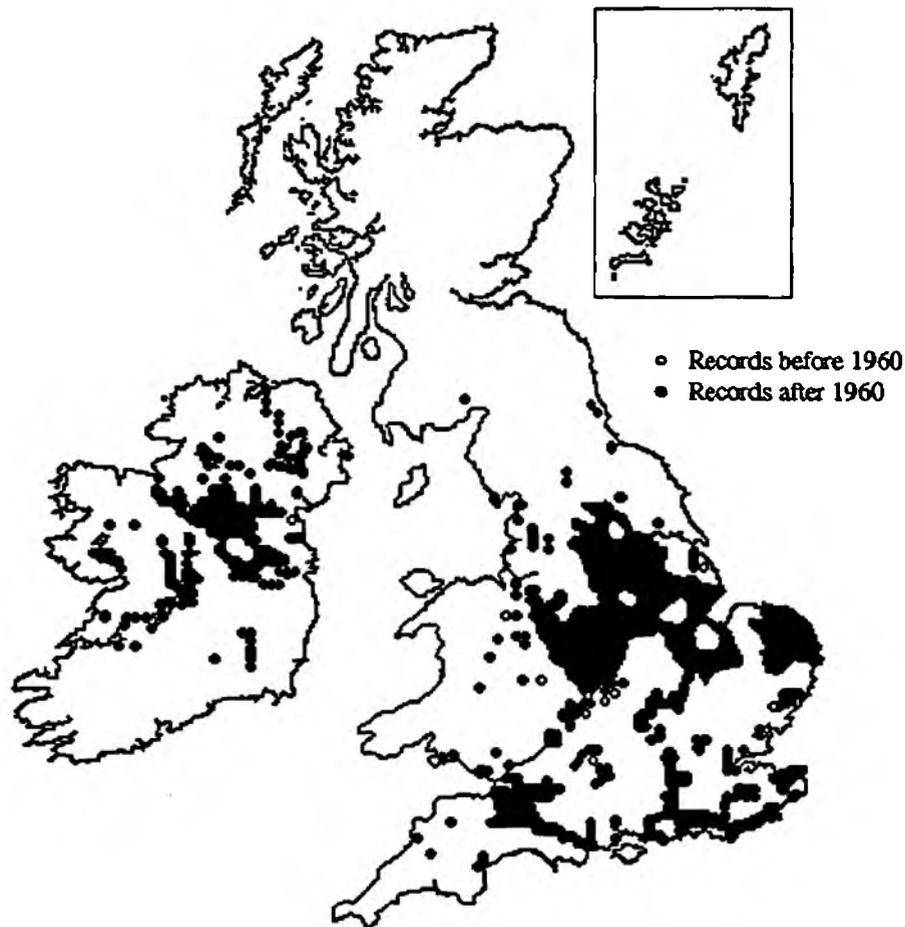


Figure 4.4 Broad distribution of bream in the British Isles (Maitland 1972)

4.5.2 Introduction

The bream is a fish of slow-flowing rivers, lowland lakes and ponds, it is markedly concave in outline and has a distinctive protrusible mouth. An adult bream weighs about 3-6 kg (Maitland 1972) and may measure 25-45 cm in length (Wheeler 1978), though these figures vary greatly between waters.

4.5.3 --Life-history

Bream spawn from May-July amongst dense vegetation in shallow water. The yellow eggs (1.5 mm Ø) are laid at night and adhere to the weeds, hatching after 3-12 days (depending upon ambient temperatures: Wheeler 1978). The rate of growth and development are both temperature-dependent, and it may be 10 years before bream in the northern limits of their range reach sexual maturity.

4.5.4 Diet

The low light levels of dawn and dusk are the times of maximum activity, while predation pressure sometimes forces the fish to take refuge during daylight. The bream feeds along the river-bed (often in shoals) swimming at an angle and sucking up insect larvae, worms and molluscs with its protrusible mouth (see Table 4.3). When feeding in shallow water, the tails of bream may be seen breaking the water surface (Wheeler 1978, Winfield *et al.* 1983).

Table 4.3 Dietary items from analysis of the gut contents of bream (Biró *et al.* 1991)

Amphipoda	<i>Dicerogammarus villosus</i>	Ostracoda	spp. indet.
	<i>Corophium curvispinum</i>	Copepoda	<i>Eudiaptomus gracilius</i>
Cladocera	<i>Alona</i> spp.		<i>Cyclops</i> spp.
	<i>Monospilus dispar</i>	Chironomidae	<i>Chironomus</i> spp.
	<i>Leydigia</i> sp.	Mollusca	<i>Anodonta cygnea</i>
	<i>Daphnia hyalina</i>		<i>Dreissena polymorpha</i>
	<i>Daphnia cucullata</i>		<i>Lithoglyphus naticoides</i>
	<i>Diaphanosoma brachyurum</i>		<i>Potamopyrgus jenkinsi</i>
	<i>Cladocera</i> spp.	Others	<i>Limnomysis benedeni</i>
	<i>Leptodora kindti</i>		

The bream is a selective feeder and it has been proposed that the factors affecting its food choice are prey size, shape, visibility and motion (both normal locomotion and escape tactics). About 95% of the diet consists of invertebrates (the remaining 5% being plant matter); and of the invertebrates 60-80% are chironomid larvae (Tatrai 1980: cited by Biró *et al.* 1991).

4.6 Barbel (*Barbus barbus*)

4.6.1 Habitat summary

- Distribution See map (Figure 4.5).
- Altitude Lowland.
- Substratum Gravel or sand.
- Flow rate Moderate.
- Flow type Upper parts of pools and lower reaches of weirpools.
- Pollution Sensitive.
- Diet Aquatic invertebrates.

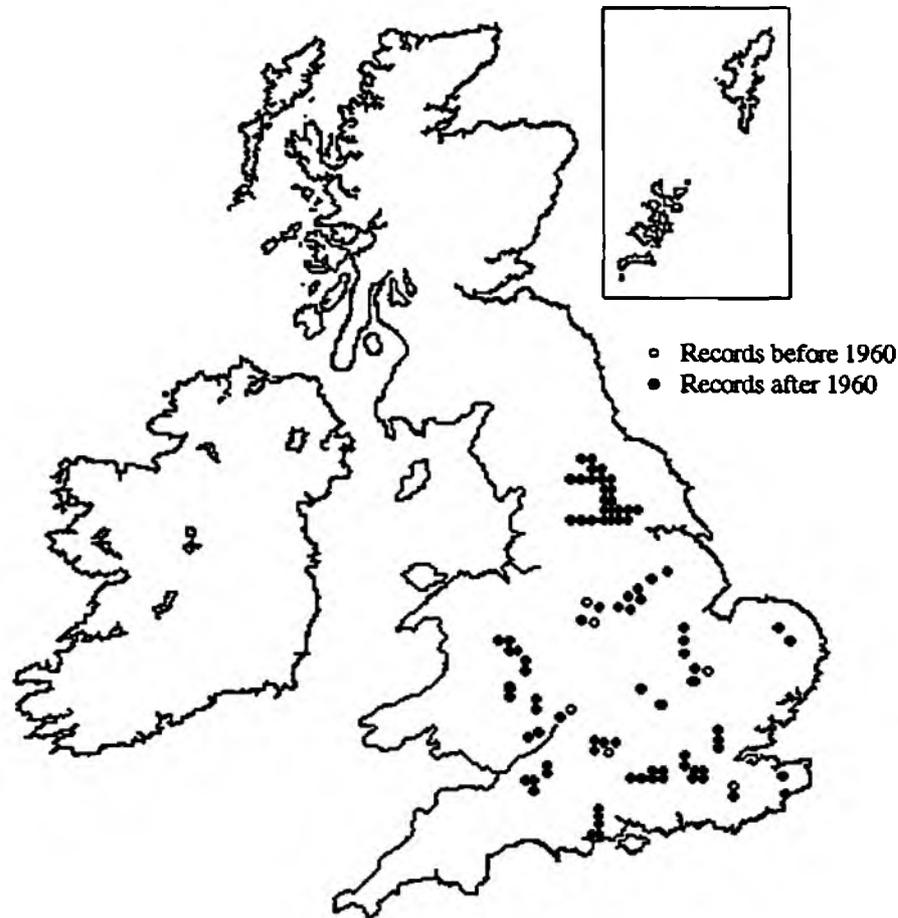


Figure 4.5 Broad distribution of the barbel in the British Isles (Maitland 1972)

4.6.2 Introduction

The barbel is a bottom-dweller which inhabits the middle reaches of lowland rivers, favouring clean gravels or sand in moderate currents (Maitland 1972). Barbel are usually found at the lower reaches of weirpools, and in the upstream sections of pools. It has two pairs of barbels on its upper lip; the dorsal surface is green-brown, whilst its sides and ventral surface have a golden yellow tint; its body is almost round in cross-section (Wheeler 1978). The average weight of an adult barbel is 2.27 kg (maximum 7.25 kg) and the average body length is 50 cm (maximum 91 cm).

4.6.3 Spawning

Barbel often migrate upstream prior to spawning, which occurs from May to July (Maitland 1972). The yellow eggs (2 mm Ø) sink and adhere to stones or lodge in interstitial spaces, hatching after 10-15 days (Wheeler 1978).

4.6.4 Diet

The barbel is a nocturnal fish which forages in shoals of similar age class, feeding upon benthic invertebrates such as insect larvae, crustaceans and molluscs (Wheeler 1978).

4.6.5 Distribution

The original range of the barbel was limited to the rivers of eastern England, between Yorkshire and the Thames but successive introductions have broadened its occurrence across England. The practice of barbel introduction began in the 1890s (prior to the formation of legislative controls) and has continued until the present day – see Table 4.4 for a list of the systems which have acquired the barbel (and the source of their stock where known). Most introductions have been of the Thames genetic stock, so future care to maintain genetic diversity is needed.

Table 4.4 Known barbel introductions (information from Wheeler and Jordan 1990)

Receiving System	Date	Source of Stock	Genetic Stock
Dorset Stour	1896	Thames	Thames
Hampshire Avon	?	Dorset Stour	Thames
Hampshire Avon	1963	Kennet	Thames
Hampshire Avon	1969	Lea	Thames
Severn (and tributaries)	1956	Kennet	Thames
Warwickshire Avon	1964	Swale	Swale
Bristol Avon (and tributaries)	1964/66/69	Kennet	Thames
Somerset Frome	?	Bristol Avon	Thames
Chew	?	Bristol Avon	Thames
Durham Wear (illegal)	1970/80s	Unknown	?
Tees (illegal)	1950s	Swale	Swale
Yorkshire Aire (illegal)	?	Other Yorkshire river	?
Calder (illegal)	?	Other Yorkshire river	?
Yorkshire Don (illegal)	?	Trent	Trent
Hull	1968	Swale	Swale
Hull	1970	Ure	?
Great Ouse	1974	Severn	Thames
Welsh Wye (illegal)	late 70s	possibly Teme	Thames ?
Welsh Usk (illegal)	?	possibly Severn	Thames ?
Welsh Dee (illegal)	?	possibly Severn	Thames ?
Ribble	mid 1970s	Unknown	?
Dane/Weaver	1983	Unknown	?
Bollin	?	Teme	Thames

4.7 Burbot (*Lota lota*)

4.7.1 Habitat summary

- Distribution See map (Figure 4.6): fenlands, rare, probably extinct.
- Depth Deep (2-3 m).
- Substratum Sand or gravel.
- Flow rate Slow.
- Pollution Sensitive, requires 5-7 mg O₂ l⁻¹
- Aquatic macrophytes Dense.
- Other cover Tree roots, overhanging banks.
- Water temperature 0.5-4.0 °C (for spawning)
- Diet Aquatic invertebrates, fish, frogs, crustaceans.

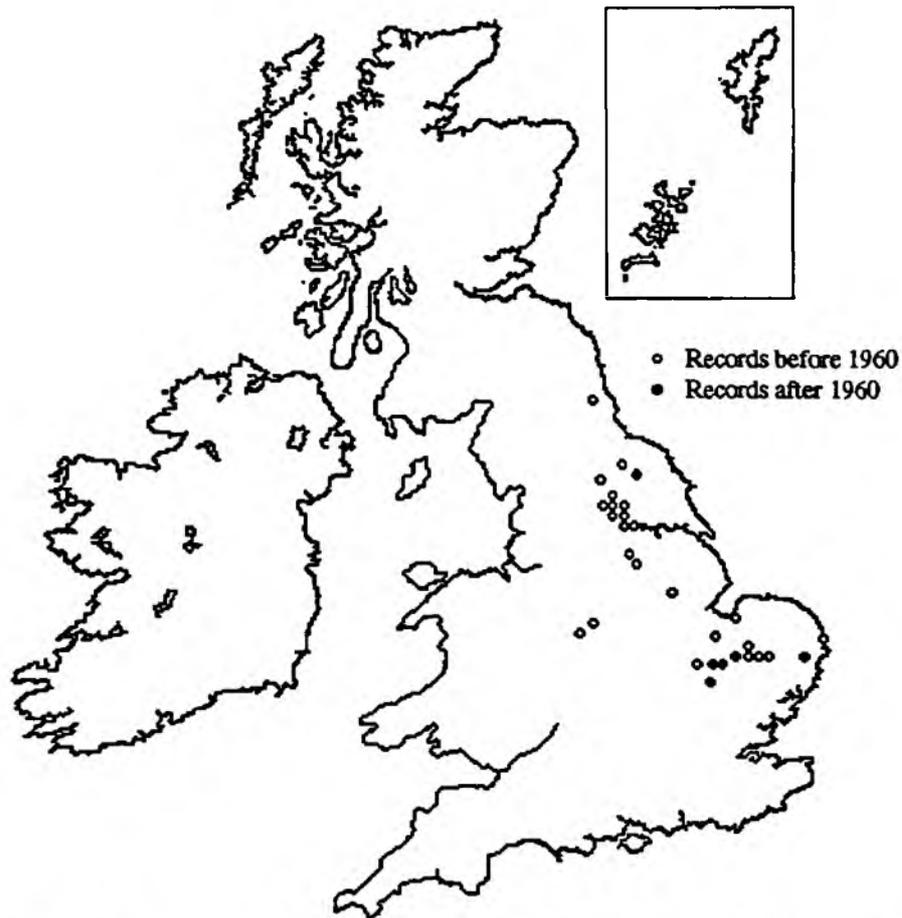


Figure 4.6 Broad distribution of the burbot in the British Isles (Maitland 1972)

4.7.2 Introduction

The burbot (*Lota lota*) is the only freshwater gadid and Britain represents the fringe of its palaeartic distribution; this fish is listed in the Wildlife and Countryside Act (1981). Identification is aided by its diagnostic single barbule beneath the chin (Walker 1964). The burbot requires clean, well-oxygenated water (5-7 mg O₂ l⁻¹; Maitland and Lyle 1991). It is found in the slow flowing water of the lower reaches of rivers and estuaries. There are no English records of burbot in enclosed water bodies (although there are records of them in lakes elsewhere).

The burbot is a dull green-brown fish with dark mottling and a yellowy underside, individuals may weigh 1-3.6 kg and may grow to 1 m in length, though 30-60 cm is its usual size range (Wheeler 1978). Some writers say it represents a helminth hazard as food – it was withdrawn from the London fish markets due to a lack of demand (Forbes 1964, Marlborough 1970).

4.7.3 Spawning and life history

The burbot spawns in the winter (December-March) at water temperatures of 0.5-4.0 °C (Maitland and Lyle 1991). Although the adults may swim from smaller tributaries into main channels there is no evidence of a substantial seaward migration to spawn (Cooper 1964). The

spawning habitat consists of shallow (2-3 m) water flowing over a clean sand/gravel bed (Maitland and Lyle 1991). The females arrive at the site first, each carrying about 3 million pale yellow eggs (1.2-1.8 mm Ø); spawning is nocturnal and communal, involving around 20 individuals (Maitland and Lyle 1991). The eggs are semi-pelagic and eventually fall to rest amongst the interstices of the gravel substratum (Maitland 1972, Wheeler 1978). The young burbot grow quickly, reaching 9-12 cm after their first year, 22-23 cm by the end of the next year and reaching sexual maturity at a length of 32-34 cm (3+ years male; 4+ years female). The life expectancy of the burbot is 10-15 years.

4.7.4 Diet

The burbot is a bottom-dweller which leads a sedentary lifestyle; during the day the young shelter amidst dense weeds and the adults are found hiding amongst tree roots, below overhanging banks and amongst water plants. Dusk and dawn represent the peak in burbot activity, when they emerge to forage. The young fish eat mainly invertebrates (benthic insect larvae, crustaceans and leeches) whilst older individuals feed largely upon fish such as the gudgeon, ruffe, perch and bullheads, supplemented by crustaceans, frogs and insects (Wheeler 1978). The dietary requirements of the burbot are distinct from those of other fished species and as such a burbot population could be encouraged without serious compromise.

4.7.5 Range

The original British range for the burbot included at least 18 large rivers in eastern England. This distribution arose from the late arrival of the burbot; it is thought to have spread eastwards through the Rhine-Thames system when Britain was still joined to the European mainland; the North Sea then effectively isolated this freshwater fish (Forbes 1964). The burbot's British range has diminished – the last specimen was recorded in 1972 and it is now thought extinct in Britain (Maitland and Lyle 1991). Without evidence of an epidemic disease or of over-exploitation, it is probably due to drainage of fenland; bioaccumulation of persistent pollutants (Marlborough 1970); and the general warming of the British climate, which would prevent the sustained cooler temperatures required for spawning (Cooper 1964).

4.8 Shad (*Alosa* spp.)

4.8.1 Habitat summary

Allis shad (*Alosa alosa*)

- | | |
|-----------------------|---|
| • Distribution | Rare, see map (Figure 4.7). Listed in the Wildlife and Countryside Act (1981). The Solway area is a possible breeding site. |
| • Altitude | Coastal and estuarine waters. |
| • Diet | Invertebrates. |
| • Negative influences | Dams and weirs obstruct migration. |
| • Disturbance | Susceptible to overfishing. |
| • Pollution | Sensitive. |

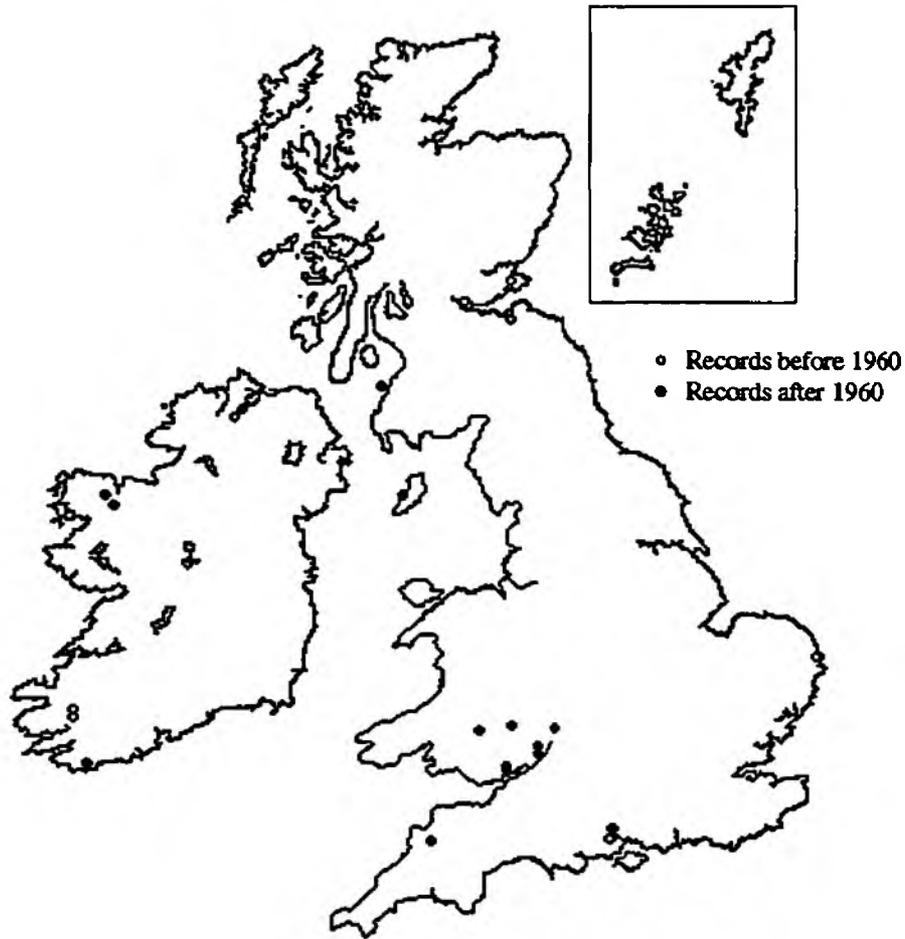


Figure 4.7 Broad distribution of allis shad in the British Isles (Maitland 1972)

Twaite shad (*Alosa fallax*)

- | | |
|----------------|---|
| • Distribution | Restricted, see map (Figure 4.8). Largely marine but enters lower freshwater reaches. |
| • Flow rate | Slow. |
| • Substratum | Pebble or gravel. |
| • Pollution | Sensitive. |
| • Diet | Invertebrates, fish. |

4.8.2 Allis shad (*Alosa alosa*)

This species is listed in the Wildlife and Countryside Act (1981) and also comes under the classification of 'vulnerable' (likely to become endangered or extinct) according to the International Union for the Conservation of Nature and Natural Resources (IUCN). This is the larger British shad species, measuring 30-50 cm in length (Wheeler 1978, Maitland and Lyle 1991). It is found in shallow coastal waters and estuaries, entering the lower reaches of large rivers during spawning in late spring.

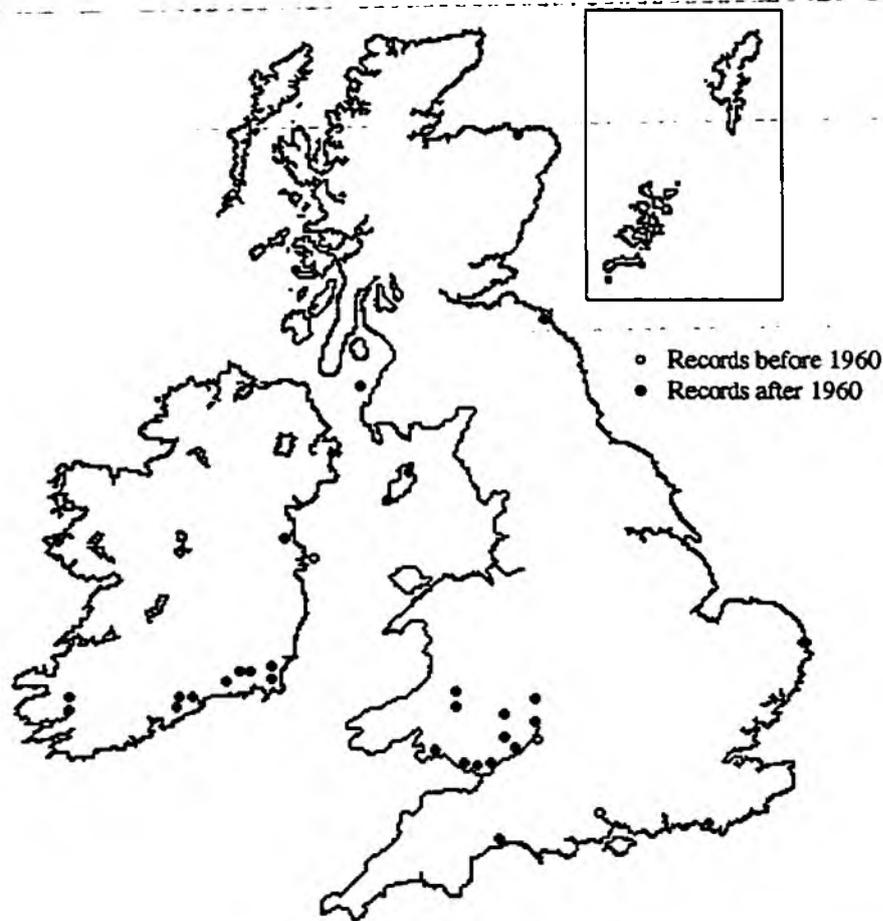


Figure-4.8-Broad-distribution of the twaite shad in the British Isles (Maitland 1972)

The allis shad was previously believed to breed in the River Severn; it is still recorded in several estuaries but there are no confirmed spawning sites (possible site in the Solway). The main threats to this fish lie in:

- Physical (e.g. dams and weirs) or chemical (pollution) barriers to migration.
- Estuarine overfishing.
- Habitat destruction by engineering works.

Allis shad spawn at night in swift running water; the adults return downstream and many die. The clear eggs (4.4 mm Ø) sink down into substratum interstices and hatch after 4-8 days. The fry measure about 10 mm on hatching; they then undergo rapid growth and reach 8-14 cm in their first year, maturing after 3-4 years at a length of 30-40 cm (Maitland and Lyle 1991).

The allis shad feeds on invertebrates (chironomids and crustaceans) in freshwater. When in saltwater the adults eat invertebrates (especially planktonic crustaceans) and fish.

4.8.3 Twaite shad (*Alosa fallax*)

The back of the twaite shad is coloured blue which changes to golden yellow laterally and becomes silvery on its ventral surface (Wheeler 1978). This is generally the smaller British

shad, measuring 25-40(-55) cm (Maitland and Lyle 1991) and weighing around 1.5 kg (Wheeler 1978). It normally lives in marine habitats to 100 m depth, though the eggs and young are found in the slow-flowing lower reaches of clean rivers close to the sea. The species is under threat from similar factors to the allis shad, although its status is less endangered. It is not a prime food fish, although it was once commercially exploited. The Rivers Wye and Severn have a reasonable run of this fish.

In April-May mature adults cease feeding and gather in estuaries prior to moving upstream. By mid-June the fish have travelled beyond the tidal reaches. Each female lays 75 000 - 200 000 eggs in water flowing over stones and gravel. The eggs lie in the gravel, and hatch after 4-6 days; and the fry then swim downstream into the waters of the upper estuary. The first years' growth is rapid (up to 5 cm in the first 6 months, reaching 10-15 cm by the end of the year); a steady growth rate of about 10 cm per year then continues until full size is reached at 8-10 years. Males mature after 3 years, females after 5 years (Maitland and Lyle 1991).

The predominant diet of the twaite shad alters with age shifting from invertebrates to fish (e.g. sandeels, young sprat and herring).

5. AMPHIBIANS

5.1 Background

Amphibians are not usually associated with lotic systems. Their inclusion in this review recognises the importance to them of slow-flowing backwaters and riparian ponds. The river corridor is often a key wetland area providing sites for both permanent and temporary pools; on a local scale, these sites may be vital for maintenance of amphibian populations and so it is important for river corridor management to consider standing water features.

The common frog *Rana temporaria* and common toad *Bufo bufo* are familiar British amphibians. Populations of both species have declined in recent years despite their perceived abundance. The endangered natterjack toad *Bufo calamita*, the edible frog *Rana esculenta* and the pool frog *Rana lessonae* may or may not be native. The marsh frog *Rana ridibunda* was introduced in 1937. Other exotic species, sometimes locally persistent, include the European midwife toad *Alytes obstetricans* (recorded in Bedford, Yorkshire and Worksop), painted frog *Discoglossus pictus* (Manchester and North London), European tree frog *Hyla arborea* (southern England), little fire-bellied toad *Bombina orientalis*, and yellow-bellied toad *B. variegata* (Devon) (Frazer 1983). There are three newt species resident in Britain: the common or smooth newt *Triturus vulgaris*, palmate newt *Triturus helveticus* and crested or warty newt *Triturus cristatus*.

Juvenile newts live on land for two or more years following metamorphosis (preferring pasture to arable land: Beebee 1980), returning to the water on sexual maturity. Newts appear to be faithful to a selected breeding site (Twitty *et al.* 1964, 1967) though the initial terrestrial phase may include dispersal. Breeding grounds are used March-July, with some exceptions. Summer quarters require sufficient prey and sites for daytime retreat (e.g. crevices, stones and boulders, long grass, or vacant burrows of other animals). It has been estimated that 9% of newt larvae will survive the period from hatching to metamorphosis (Bell 1970); and that on reaching land, 80% of juveniles and 50% adults are lost per annum (Frazer 1983). Heavy losses through predation (e.g. by grass-snakes, water shrews, fish and water birds) may prevent success of a population of newts in a particular pond (Frazer 1983).

The majority of information concerning the ecology and behaviour of amphibian species is limited to spawn site characteristics and selection; whilst other aspects concerning diet and foraging behaviour, hibernation and predation have received less attention. A major research project under the AFRC/NERC Agriculture and Environment research programme, carried out by Leicester University and Leicester Polytechnic, is due to terminate at the end of 1992. This will provide new information about habitat requirements of newts in British farmland and riparian habitats and will thus update the information contained in this review.

5.2 Smooth / common newt (*Triturus vulgaris*)

5.2.1 Habitat summary

- | | |
|----------------------|--------------------------|
| • Distribution | See map (Figure 5.1). |
| • Flow regime | Lentic. |
| • Pool area | <100 m ² |
| • Water chemistry | Cation-rich, hard water. |
| • Aquatic vegetation | Abundant macrophytes. |

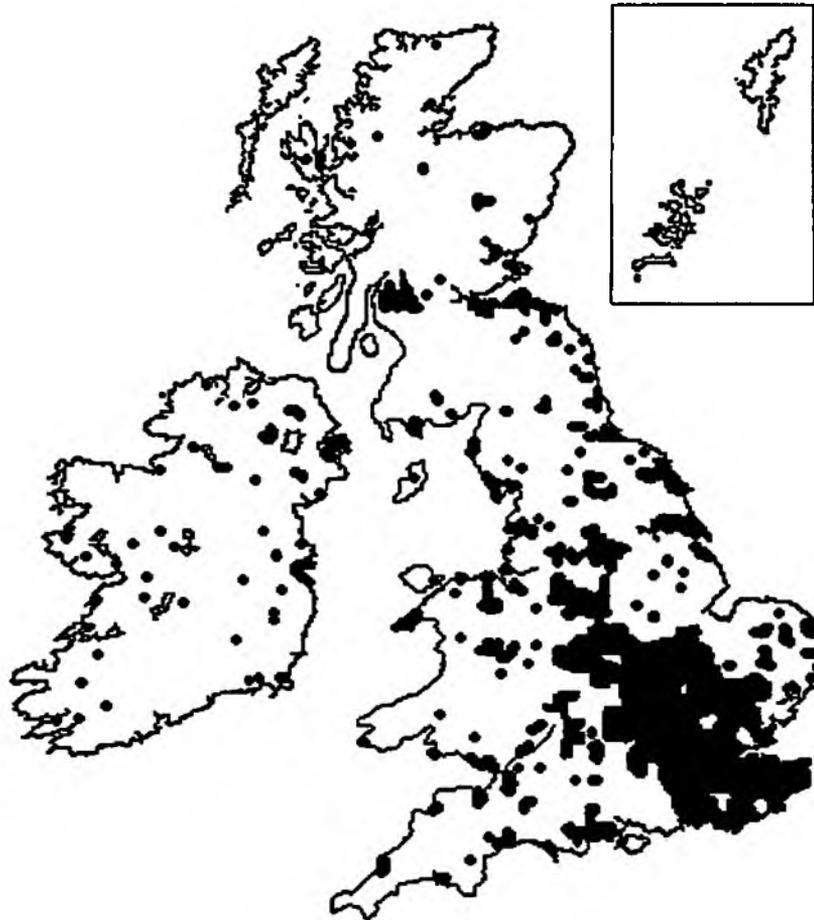


Figure 5.1 Broad distribution of the smooth newt in the British Isles (Frazer 1983)

5.2.2 Breeding

Cooke and Frazer (1976) found that both smooth and warty newts commonly select 'hard water' sites (high concentrations of calcium carbonate). They suggested that choice of site and subsequent spawning is stimulated by metabolites of algae specific to water of that chemistry.

The smooth newt tends to choose small pools (surface area $<100 \text{ m}^2$) with abundant aquatic weeds. Adults have been recorded entering breeding pools in Leicestershire (Bell 1970) and Epping Forest (Malenoir 1963) as early as beginning of February, although in the latter case breeding colours were not assumed until April. The numbers observed at the Leicestershire site peaked around mid-April, and the larvae metamorphosed in late July-August – although larval over-wintering is reported to occur regularly (Bell 1970).

5.2.3 Diet

Newt larvae feed on aquatic invertebrates. Adults are known to eat slugs and snails, worms, various other invertebrates, frog spawn, and the tadpoles of both frogs and other newt species. The smooth newt finds toad tadpoles unpalatable (Frazer 1983, Reading 1990).

5.2.4 Hibernation

In the autumn, smooth newts move from their usual land shelters and bury themselves as a protection against the cold (Frazer 1983). Smooth newts have been found hibernating in the mud and crevices at the bottom of pools (Bell 1970). If the conditions are suitable (correct soil humidity, avoiding wet ground) they may remain in their summer quarters, deeper underground, for winter hibernation.

5.2.5 Range

The smooth newt occurs throughout Britain and is the only newt to be found in Ireland (Figure 5.1: cf Figures 5.2 and 5.3). Whilst all three newt species coexist locally, the smooth newt and great crested newt are generally found at lower altitudes (Bell 1970).

5.3 Great crested / warty newt (*Triturus cristatus*)

5.3.1 Habitat summary

- Distribution See map (Figure 5.2).

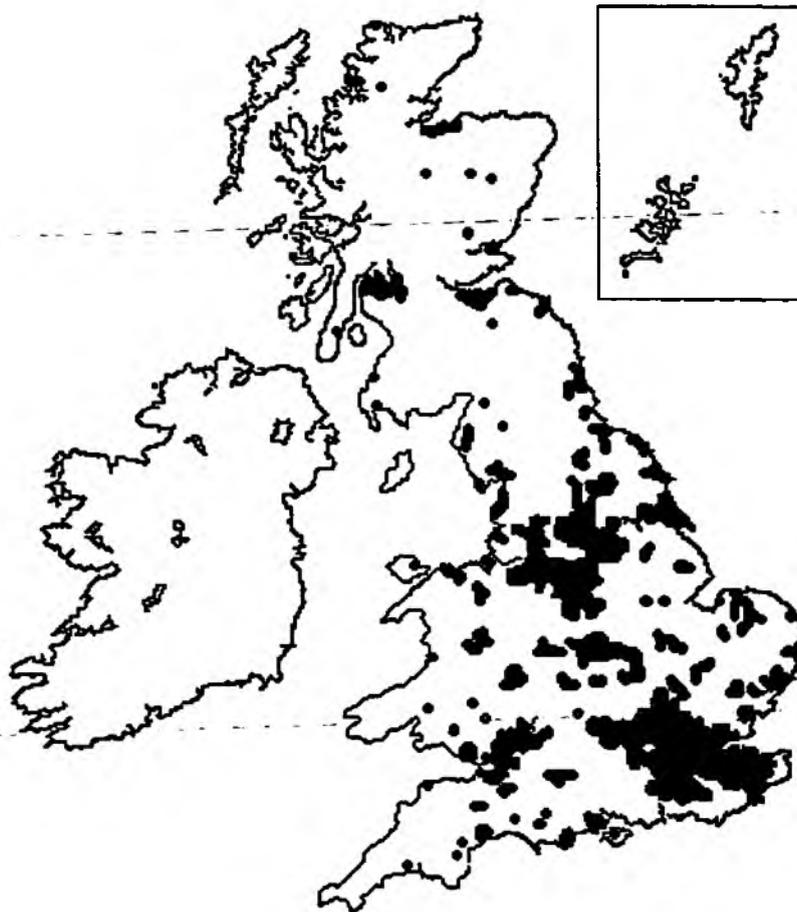


Figure 5.2 Broad distribution of the great crested newt in the British Isles (Frazer 1983)

- Flow regime Lentic.
- Pool depth ≥30-55 cm.
- Water chemistry Cation-rich, hard water.
- Aquatic vegetation Limited emergent macrophytes.

5.3.2 Breeding

The water chemistry of breeding sites chosen by the great crested newt is similar to that of sites chosen by the smooth newt (Cooke and Frazer 1976: and see Section 5.2.2). Their preferences differ when choosing the physical characteristics of a spawning site; the great crested newt often selecting deeper pools (at least 30-55 cm deep: Frazer 1983) with a high proportion of open water at the pond surface and little emergent vegetation. Cooke and Frazer (1976) nevertheless observed that the two newt species often co-exist, albeit with a degree of spatial separation; and that the great crested newt is seldom found in the absence of the smooth newt.

From observations in Leicestershire, Bell (1970) suggested that breeding activity commences approximately three weeks later than that of the smooth newt (*T. cristatus* peak breeding numbers observed late April to early May). Adults commonly return to the water throughout February-March and remain there for approximately two months before breeding (Frazer 1983). Metamorphosis generally occurs in July-August but timing depends upon ambient temperature. Eggs from later layings may produce larvae which over-winter in the breeding pool and metamorphose the following year.

5.3.3 Diet

Great crested newts generally feed on whatever is most abundant locally (Frazer 1983). They feed upon a variety of aquatic invertebrates, worms, and frog tadpoles. It has been suggested that they take larger prey than other newt species in the same pond (Avery 1968).

5.3.4 Hibernation

From late summer to spring, great crested newts are found under stones or in the soil where they feed on invertebrates and then hibernate (Frazer 1983).

5.3.5 Range

The great crested newt has a widespread distribution, similar to that of the smooth newt. It is found from the south of England to the north coast of Scotland, with a high recorded density in East Anglia; but is absent from Ireland.

A recorded numerical decline of the great crested newt may be partially attributed to a 75% decrease in the use of ponds on agricultural land for breeding, as a result of increased pollution (Beebee 1975).

5.4 Palmate newt (*Triturus helveticus*)

5.4.1 Habitat summary

- | | |
|----------------------|--|
| • Distribution | See map (Figure 5.3) |
| • Flow regime | Lentic. |
| • Pool area | <100 m ² |
| • Water chemistry | Cation-deficient, especially low [K ⁺], acidic (pH c. 3.9) |
| • Aquatic vegetation | Abundant macrophytes. |
| • Altitude | 0-880 m above sea level. |

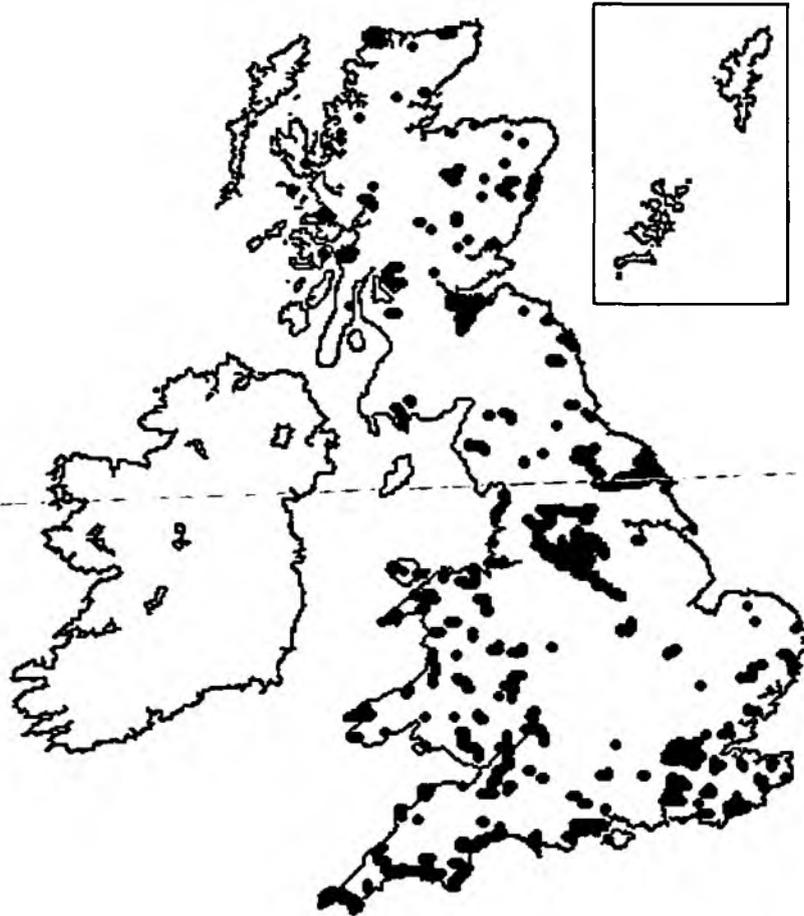


Figure 5.3 Broad distribution of the palmate newt in the British Isles (Frazer 1983)

5.4.2 Breeding

Palmate newts generally prefer pools of soft, acidic (pH about 3.9), cation-deficient water; especially those with low potassium and calcium (Cooke and Frazer 1976). Although the palmate and smooth newts may be separated by the chemical composition of their breeding grounds, the physical characteristics of preferred sites appear to be similar (i.e. small pools

supporting abundant macrophytes). Yalden (1965) found there to be no evidence of correlation between palmate newt distribution and either pH or pond size in the London area.

5.4.3 Diet

The diet of the palmate newt is the same as that of the smooth newt (Section 5.3.3).

5.4.4 Hibernation

In montane areas palmate newts may spend the entire year in the water, only leaving pools if they dry up. Elsewhere a small percentage may overwinter in the water but most act similarly to other *Triturus* species (Frazer 1983).

5.4.5 Range

The palmate newt is generally more dominant in upland areas (Cooke 1975). It has been described as a 'montane' species (Smith 1951) although its distribution, ranging from sea level to 880 m, suggests that its habitat choice may be primarily influenced by some factor other than altitude. Whilst there appears to be no systematic preference between ponds in montane areas, there are pools in the lowland environment in which the palmate newt is never seen (Frazer 1983).

5.5 Common Frog (*Rana temporaria*)

5.5.1 Habitat summary

- | | |
|-------------------|---|
| • Distribution | See map (Figure 5.4) |
| • Flow regime | Lentic, possibly lentic habitats on rivers. |
| • Pool depth | Shallow margins (15-70 cm) |
| • Water chemistry | High [K ⁺], high January / low April [PO ₄ ³⁻], pH > 5.0 |
| • Light level | Direct sunlight. |

5.5.2 Juvenile stage

There is no evidence to suggest a difference in lifestyle between adult and juvenile life-stages, except during the breeding season.

It takes approximately three years for the common frog to attain sexual maturity. This has been supported by investigation into the life history of the bladder parasite *Polystoma interrimum*, which also reaches maturity after 3 years in readiness to lay its eggs along with its host (Savage 1961). During the juvenile phase there is no stimulus to return to a breeding site and it is thus free to travel across areas devoid of ponds, establishing a new territory in time for sexual maturity.

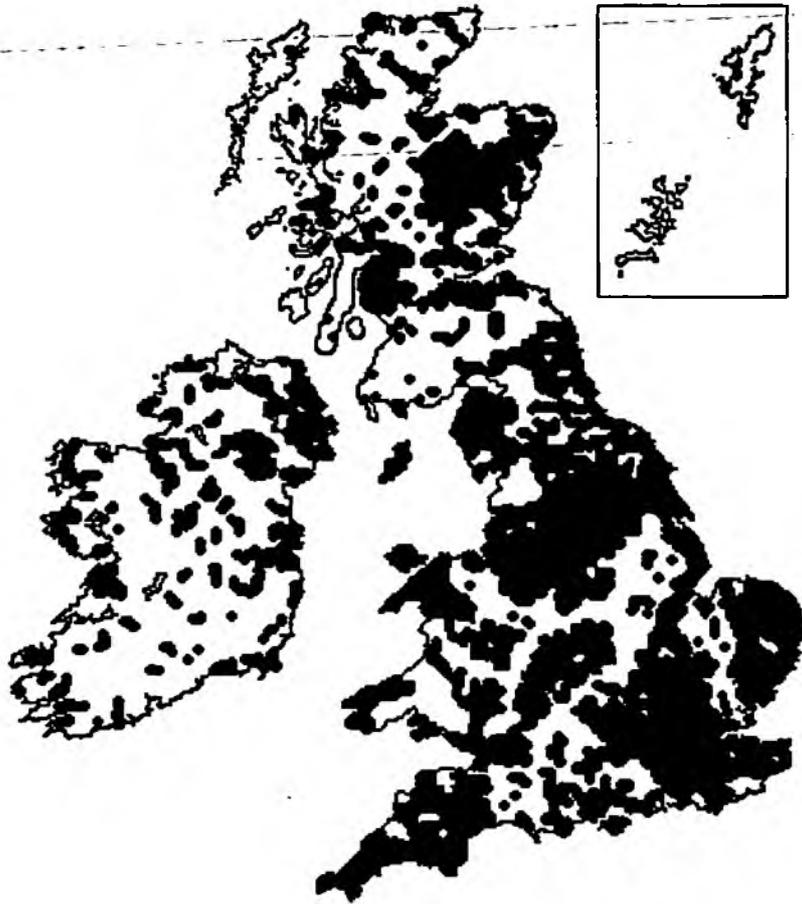


Figure 5.4 Broad distribution of the common frog in the British Isles (Frazer 1983)

5.5.3 Site selection

Having reached maturity, the adult frog exhibits a distinct behaviour pattern. The year is divided into three phases of activity (Oldham 1963):

- Migration to preferred spawning sites for the breeding season.
- Dispersal to summer feeding areas, usually moist grassland.
- Hibernation through the colder months, both on land and underwater.

There is limited information on the site requirements of the common frog during its summer and winter phases. Most study has been of the characteristics required of a successful spawning site.

Whilst some authors doubt that selectivity is involved when finding a suitable breeding site (Perkins 1973), it is generally agreed that active selection occurs. A potential site with poor access (e.g. isolated by arable fields) is unlikely to be used. Spawns are most commonly deposited in the shallow margins of small ponds, 15-70 cm deep (Oldham 1963); often in the warmest part of the pond, receiving full sunlight (Frazer 1983). Areas of deeper water may be selected where mats of weed present a suitable depth (Savage 1961). Cooke (1975) suggested that by selecting the warmest part of the pool, the development of the spawn is accelerated, and the cumulative risk of predation is reduced. In this position algae will be metabolising more rapidly than in the cooler regions of the pool, increasing the level of the attractant glycollic acid

(Frazer 1983). Temporary habitats (such as shallow pools and water-logged furrows) offer spawning sites free from competition and predation; but the entire cohort may be lost if the pool dries out prior to their metamorphosis.

Spawn is rarely observed on exposed shores or in flowing water, although sheltered in-stream sites (backwater, bridge, or ford) may provide suitable conditions. In addition, there should be a plentiful supply of algae and zooplankton available on which the tadpoles may feed – for this reason, the ionic composition of the water and local geology may indirectly influence the choice of site. Savage (1961) reported significant associations between favoured spawning pools and high levels of potassium, along with high January levels of phosphate (facilitating rapid algal growth) falling to a low level at time of spawning. The level of phosphate may increase after a rainfall event as a result of run-off into the pool. The common frog will tolerate pH as low as 5.0 (Beebee and Griffin 1977).

5.5.4 Homing behaviour

There has been much speculation concerning the existence of a homing drive and the ability of individuals to return to favoured sites (for spring spawning, summer foraging, and winter hibernation). One complicating factor is the possible proximity of each of the three localities; and consequent difficulty of detecting migration. Studies of homing behaviour have tended to concentrate on the breeding phase, when migration to a recognisable colony is most easily quantified.

It is generally believed that some site fidelity appears to exist in the common frog; but less than that of the common toad *Bufo bufo* (Perkins 1973, Cooke 1975). The common frog also appears far less selective in its choice of spawning site. Experiments to demonstrate the homing behaviour of the common frog most commonly involve capture from a breeding colony, tagging, displacement, release and tracking of individuals (Oldham 1963, Perkins 1973). From his sample of 99 male common frogs taken from two connected breeding pools, approximately 35 m apart, Oldham (1963) concluded that the individuals showed a greater tendency to return to their pool of origin than to another site, which may in fact be closer than the 'home' pool. He further noted that at least 16 frogs passed a site containing breeding frogs when returning to their home pool.

Savage (1961) suggested that olfactory signals (related to events occurring within the water body, and in particular to the change within the algal community of a pool) stimulate migration and act to guide individuals to the breeding site. He argued that the odour of a particular algal community is distinctive and detectable from some distance. In experiments involving captive *Xenopus laevis* and algae (*Chlamydomonas pulsatilla*), Savage identified glycollic acid as a homing attractant.

Evidence to support fidelity to a particular location within a favoured breeding pool, observed by Savage (1961), has been questioned (Bell 1970). The breeding colony may choose to relocate within a traditional site in response to a change in water level and/or the local vegetative community.

5.5.5 Spawning

After location of a suitable breeding site, recorded dates of breeding activity range from the end of January through to August, apparently exhibiting spatial variation (Savage 1961: and see Figure 5.5).

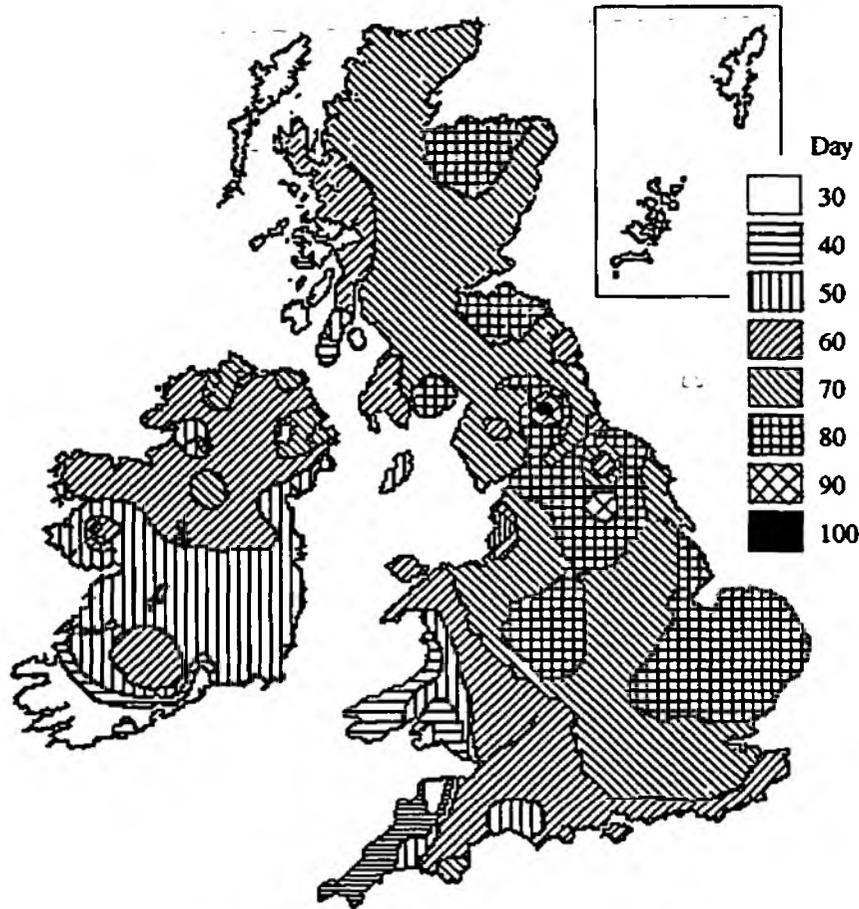


Figure 5.5 Date of spawning of the common frog in the British Isles (Frazer 1983)

Despite this extended breeding period, spawning in a single pool is so short (about 12 days) that Savage (1961) has described it as an 'explosive' event. Whilst it is recognised that the breeding cycle is under the control of hormones, Savage suggested that onset of sexual activity within a pool is not triggered by individuals' physiology. Instead he offered the hypothesis that a single external olfactory signal (similarly to migration) is responsible for inducing ovulation, subject to physical conditions such as weather.

The common frog is polygamous, males securing more than one female subject to their success in dislodging rival males. Competition between males is high and it is important for them to arrive at the site prior to the commencement of breeding. Once at the breeding site the individuals begin to pair (some may arrive at the pond already paired), and remain 'in amplexus' until such time that the spawn has been deposited. There may be a time-lag between pairing and spawning. This is seen by Savage (1961) as evidence supporting his olfactory-stimulus hypothesis (a change of algal 'smell' triggering sexual activity), whilst Frazer (1983) interpreted such delay as a result of water temperature fluctuation.

Ejection of the eggs from the female is aided by abdominal pressure applied by her upper limbs (Savage 1961). After spawning the female is no longer passive; but instead exhibits similar behaviour to that of the male, vocalizing to stimulate release by the male. The sexes then separate, often remaining at the pond margins (Perkins 1973). The males congregate for longer than the females (Bell 1970) and do not travel as far afield (Hazelwood 1969: cited by Frazer 1983). Many individuals disperse, under cover of the new growth of grass and adjacent

vegetation, whilst the remainder may choose to stay in the damp environment offered by the marginal macrophytes as the water level of the pond drops.

5.5.6 Diet

Frogs fast during the breeding season, after which they will leave the water to feed (Frazer 1983). The common frog will take any suitably sized invertebrate and the dietary composition changes with the abundance of insects (Frazer 1983). Smith (1951) has identified molluscs (especially slugs) as a major dietary component, but this is influenced by season and geographical location (Table 5.1).

Diurnal feeding involves little active foraging; the frog waits to take prey that passes close to its hiding place, emerging from shelter only at night or in wet conditions to search for invertebrates. There can be a diel change of feeding area in response to distributions of diurnal and nocturnal prey (Perkins 1973).

Frazer (1983) stated that studies of the intestinal contents of the common frog have shown that they feed entirely on land. This contradicts evidence suggesting that underwater feeding occurs during submerged hibernation (Savage 1961): stomach contents of frogs found in January and February were seen to contain the larvae of aquatic insects. Aquatic feeding is also implied by the fact that the intermediate host of the intestinal parasite *Acanthocephalus ranae*, found in the common frog, is the water louse *Asellus aquaticus* (Smith 1949).

Table 5.1 Dietary items of the common frog (various sources ¹)

Location	Cornwall	Ireland	Cumbria (adults)	Cumbria (young)
Sample size	17	70	359	14
Total no. food items	228	665	6681	?
	% of food items			
Collembola	4.8	10	0.7	13
Orthoptera		0.1		
Hemiptera	6.6	6	1	3
Neuroptera		2		
Mecoptera		0.1		
Lepidoptera (adults)	1.8			
Lepidoptera (larvae)	11.4	8	20.7	
Diptera	9.2	19	29.9	18
Hymenoptera	4.8	6	6.5	10
Coleoptera	12.3	20	10.3	2
Arachnida	2.2	17	14.5	
Acari	1.3		0.2	
Oligochaeta	0.9	1	2.1	
Isopoda	12.8		0.2	
Opiliones	3.9			1
Chilopoda	3.5	0.8	0.3	
Myriapoda		1		
Mollusca	25.4	8	11.1	

¹ Data: Cornwall (Smith 1951, Frazer 1983); Ireland (Blackith and Speight 1974); Cumbria (Houston 1973)

5.5.7 Hibernation

The majority of frogs return to an area close to their hibernating quarters by late September or October (Frazer 1983). The common frog is well adapted for both terrestrial and

subaqueous hibernation, due good cutaneous circulation at low temperatures. Most recorded observations are of underwater hibernation (tadpoles as well as adults: Bell 1970); but this may be because such individuals are more readily visible, whilst on land they may hibernate well-hidden within sheltered crevices. They tolerate low temperatures very well, and have been revived from ice (Savage 1961).

The duration of hibernation is influenced by prevailing climatic conditions and altitude. Otherwise, studies concerning the duration of hibernation have usually concerned captive frogs and may be too far divorced from field conditions (Savage 1961).

5.5.8 Mortality

Savage (1961) estimated over 99% mortality of tadpoles and early juveniles. Predation of spawn and tadpoles is generally high and is possibly the most important controlling factor in population size. Predation may locally eliminate an entire cohort. It is generally assumed that many species associated with the aquatic environment predate spawn and tadpoles, but no author cited in this review gives a general account. Savage (1961) observed predation by moorhens, and large invertebrate predators such as dragonfly larvae may seize tadpoles. Other reported predators are leeches (Carpenter 1953) and newts (Reading 1990). The palmate newt can distinguish between palatable tadpoles of the common frog and those of the common toad, suggesting that tadpoles must be a significant dietary component.

Heavy mortality occurs at metamorphosis, when large numbers of juvenile frogs drown (Savage 1961). The frogs should be able to exchange gases cutaneously underwater; but metamorphosis is often at times of high water temperature, with least dissolved oxygen.

Mortality rates are usually lower after metamorphosis, despite a variety of potential predators (hawks, owls, crows, gulls, ducks, terns, herons, hedgehogs, stoats, weasels, badgers, otters, rats: Smith 1951). The water shrew (*Neomys fodiens*) may take adult frogs and other amphibians; the polecat (*Mustela putorius*) and the medicinal leech (*Hirudo medicinalis*) also feed on frogs (Frazer 1983). Although these species do not rely upon the common frog as a main food source, it may provide an important dietary contribution seasonally, and the effects of predation on a colony of breeding frogs may be considerable. The grass-snake (*Natrix natrix*) hibernates in winter and shares a similar habitat with the common frog, on which it is a frequent predator (Savage 1961).

Man is a capable predator of the common frog; for laboratory material (Savage 1961) or for curiosity (removal of spawn and tadpoles). Furthermore, the creation of landscape 'barriers' (including roads, railways and embankments) has consequences which are both immediate (traffic-related mortality; extinction of sub-populations) and long-term (isolation encourages inbreeding and genetic drift (Reh and Seitz 1990).

To reduce mortality and isolation, barriers across known migratory routes can be equipped with collecting fences and tunnels; important breeding sites can be linked by ditches, or by neighbouring areas of meadow. Existing populations may increase if sites are carefully managed or new, accessible sites created.

5.6 Common toad (*Bufo bufo*)

5.6.1 Habitat summary

• Distribution

See map (Figure 5.6).

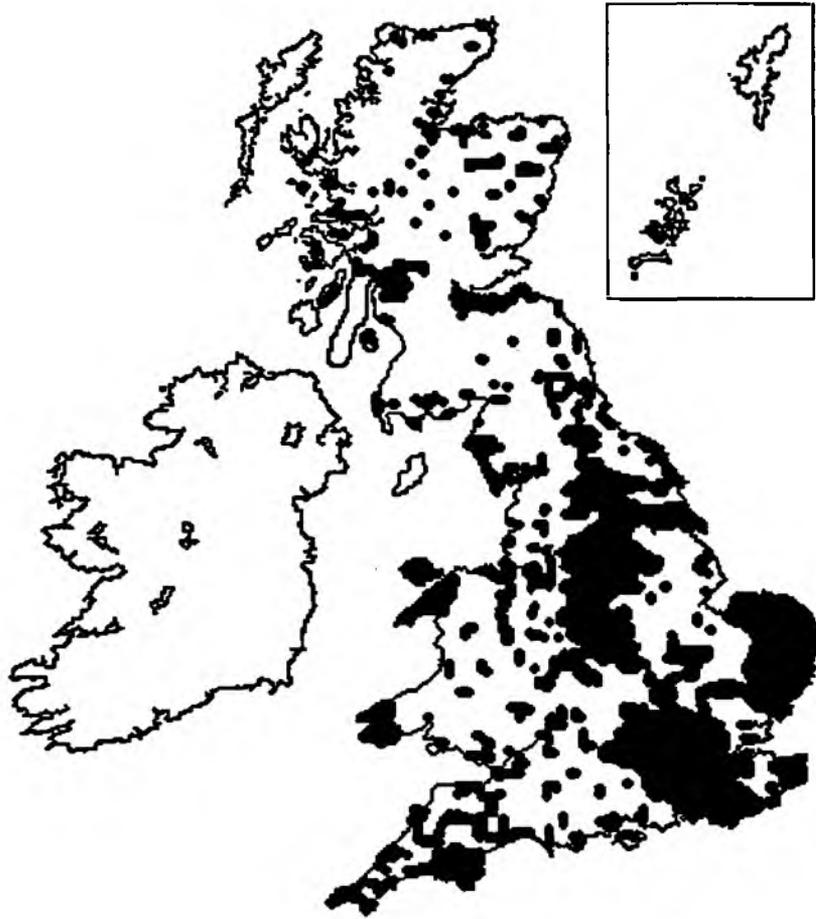


Figure 5.6 Broad distribution of the common toad in the British Isles (Frazer 1983)

• Flow regime	Lentic.
• Pool depth	Mean 40 cm, usual range 18-46 cm, extreme 4-5 m
• Water chemistry	Acidic.
• Aquatic vegetation	Requires macrophytes or firm substrata.
• Hibernation sites	Woodland, disused mammal burrows.

5.6.2 Site selection

Since the 1950s a reduction of natural spawning sites has led to adoption of garden ponds (Cooke 1975). However, the requirements of the common toad are different from those of the common frog. The toad tends to spawn in deeper water: most often around 40 cm (Frazer 1983); generally in the range 18-46 cm (Cooke 1975); but exceptionally 4-5 m (Frazer 1953: cited by Frazer 1983). Macrophytes (or a firm substrata) are required, from which to support sessile spawn strings. The toad will also tolerate more acid conditions (Jones 1939).

Common toad tadpoles are distasteful to a variety of species that predate frog tadpoles (Cooke 1975, Reading 1990). The toad would therefore not derive as much benefit as the frog from depositing its spawn in a temporary, predator-free pool – which might dry out prior to metamorphosis.

5.6.3 Homing behaviour

The common toad usually exhibits considerable selectivity and site fidelity; more so than the common frog (Yalden 1965, Bell, 1970). This has been observed during an experiment involving translocation of pairs of toads and frogs whilst in amplexus (Perkins 1973). On release, pairs of toads dispersed in search of an acceptable site whilst the frogs spawned immediately. Despite these translocation experiments, there is little evidence to suggest whether *B. bufo* homing is achieved by individuals following algal scent; through knowledge of the territory; by using an unidentified internal 'compass'; or by tracing the calls of earlier arrivals (Frazer 1983), although the weak vocalizations are probably not traceable over much distance (Heusser 1968a). The precise location of spawning within a pool may vary between years.

5.6.4 Spawning

In Leicestershire, common toads cease hibernation in late March, migrate during late March to early April, and spawn in April-May (Bell 1970). Emergence and migration of toads has been related to a spring temperature threshold of 5-6 °C. If the temperature falls during migration, the toads may return to earth. On arrival at the breeding site the toads take shelter in emergent vegetation or in the pool substratum (Frazer 1983). Some toads may arrive already in amplexus, whilst others travel singly, possibly covering several miles over a number of nights.

Unpaired males await the arrival of females to the pool, whereupon several males may attempt to seize an unpaired female. The water temperature of the breeding pond usually rises to 9 °C before the spawn string is deposited on vegetation. If vegetation is not available, twigs or rubbish may be used (Frazer 1983). The females depart after spawning but the males to remain for several days after the last of the eggs have been produced.

5.6.5 Diet

The common toad does not usually feed prior to the breeding season. Throughout the summer the toad takes shelter during daylight hours in damp surroundings (in holes, beneath stones, or buried) avoiding excessively dry conditions that might cause dessication, and forages most commonly by night. Frazer (1983) suggested that toads are most active on rainy nights when the temperature exceeds 11 °C. They are opportunistic feeders and take a wide variety of live macroinvertebrates. Prey-size has some influence on choice; and there is some evidence of attraction to prey by scent (Frazer 1983). The common toad will actively avoid unpalatable wood-ants and insects with warning colouration.

5.6.6 Hibernation

Toads have been observed migrating to hibernation sites close to their spawning pond during August-September (Heusser 1968b: cited by Frazer 1983). It is common for the species to enter hibernation between September-October in forests and copses, beneath old timber, within self-dug holes or in the burrows of small mammals (Frazer 1983). Bell (1970) suggested that *B. bufo* does not hibernate underwater, although a few records exist of individuals hibernating in mud substrata (Waddington 1952: cited by Frazer 1983).

5.6.7 Mortality

The spawn of the common toad is eaten by common frog tadpoles. This may provide an explanation for sympatric niche separation of the species (Heusser 1970). Toad tadpoles are

distasteful to many predators of the common frog; an exception to this is the great crested newt (*Triturus cristatus*) that breeds in deep pools and, unlike other British newts, complements its diet of frog tadpoles with those of *B. bufo*. Palatability of adults is reduced by unpalatable skin secretions but some predation by hedgehogs, corvids, and grass snakes still occurs.

During hibernation, juvenile toads are more vulnerable than adults (both to predation and to severe weather conditions) because of their smaller size and less careful positioning, often nearer the ground surface. Site fidelity increases the risk of population extinction, should that site be destroyed (Yalden 1965). The common toad is also highly susceptible to traffic-related mortality, as a result of a strong homing instinct to established spawning sites which become increasingly isolated by roads. One observer noted high adult losses both on the way to a site and on dispersal, which would probably be repeated in each year (Squires 1964).

5.7 Natterjack Toad (*Bufo calamita*)

5.7.1 Habitat summary

- Distribution See map (Figure 5.7).



Figure 5.7 Broad distribution of the natterjack toad in the British Isles (Frazer 1983)

- Flow regime Lentic.
- Pool depth Shallow (8-18 cm) preferred.
- Water chemistry pH > 4.75
- Soil type Sandy, light consistency (coastal)

5.7.2 Site selection

The natterjack toad mostly inhabits sandy coastal areas, where it can easily burrow; or localities characterised by light soil and warm, shallow breeding ponds. It requires only a few centimetres of fresh or brackish water to spawn, though a depth of 8-18 cm is preferred. Metamorphosis requires a water temperature of around 25 °C (Matthias 1971). Beebee and Griffin (1977) suggested increased acidity of ponds over the past 40 years (from acid precipitation) has contributed to the decline of suitable breeding sites; especially in heathlands, where ponds are frequently below pH 4.75. The natterjack toad changes its precise breeding ground every few years, perhaps in response to changing conditions in the pond (commonly drying out as a result of ecological succession or fall in the water table (Frazer 1983).

5.7.3 Spawning

Natterjack toads emerge from hibernation and travel to a breeding site in late March to June (in the north) or April to early August (south), with the exact timing depending upon weather conditions (Frazer 1983). They congregate at a breeding site, emerging from shelter to pair during or after rainfall. Unlike the common toad, the natterjack vocalizes loudly; and may be heard calling during the breeding season from the pool margins. Spawning activity begins during inclement weather conditions, when the water temperature is between 14 °C and 25 °C (most usually 14-18 °C) and is complete within a few hours (Frazer 1983).

5.7.4 Diet

After up to a month at the breeding site, the toads disperse individually to their summer quarters and dig a daytime retreat, 25 cm or more beneath the surface. They do not eat until the temperature has risen to 11-12 °C, when they forage for crepuscular prey (Frazer 1983). If the summer site is situated coastally, stranded sea-weed provides a local source of invertebrates. Prey items include insects (e.g. moths), spiders, woodlice, worms and molluscs; a similar diet to the common toad (Frazer 1983). The natterjack will not leave its shelter during the day in response to rainfall, unlike the common toad which takes advantage of emerging worms.

5.7.5 Hibernation

Hibernation usually occurs singly in the burrow, 25-50 cm below ground level. They have also been found hibernating in an abandoned sand martin nest and in larger rodent or rabbit burrows, in which they may congregate in small numbers (Smith 1951).

5.7.6 Mortality

Known predators of natterjack tadpoles include the larvae of the great diving beetle (*Dytiscus marginalis*) and adult smooth newts. If food availability is low within the pond then cannibalism can occur. Adult natterjack toads are taken by rats and waterbirds (including heron, widgeon and black-headed gull).

The characteristically shallow ponds used by the natterjack toad as a breeding site are at risk of drying out prior to metamorphosis of the tadpoles. Conservation efforts may therefore include the sanctioned relocation of spawn to deeper sites, or deepening of existing slacks and ponds. Collection of natterjack toads is illegal under the Wildlife & Countryside Act.

5.7.7 Range

The natterjack toad formerly inhabited a broad band from Dorset, through Hampshire and Surrey, to East Anglia (Frazer 1983). The urbanization of the south-east and more intensive agricultural practices in rural areas, have restricted its distribution to pockets of sandy coastal and heathland areas.

6. BIRDS

6.1 Kingfisher (*Alcedo atthis*)

6.1.1 Habitat summary

- Distribution See map (Figure 6.1)

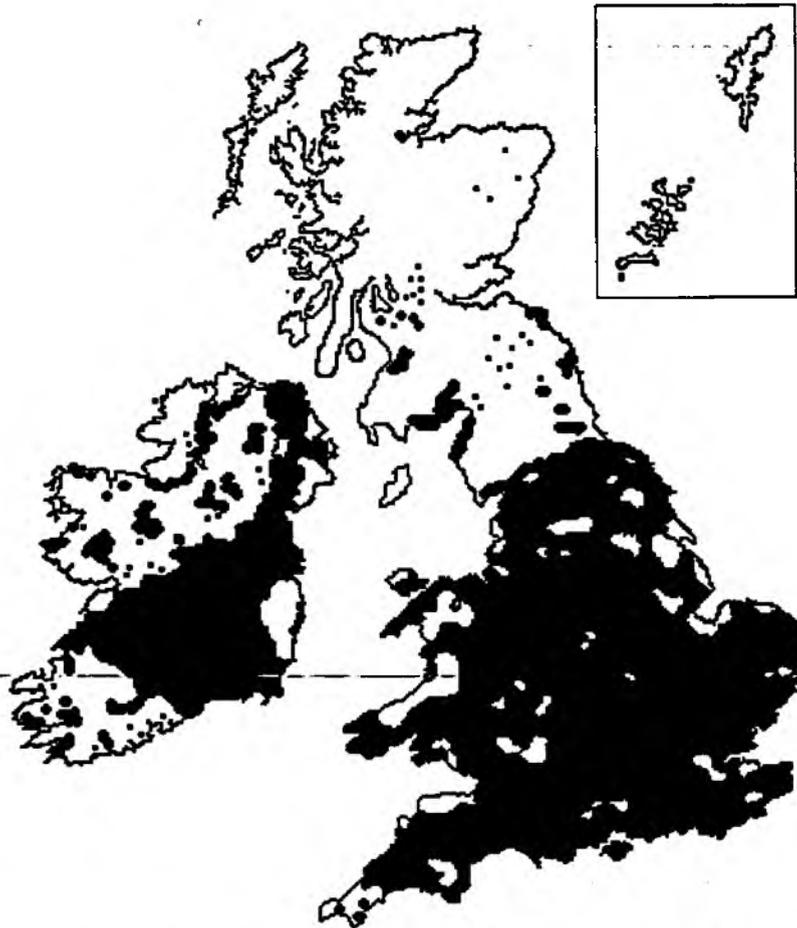


Figure 6.1 Broad distribution of the kingfisher in the British Isles (Sharrock 1976)

- | | |
|-------------------|--|
| • Flow regime | Natural features e.g. bays, junctions, bends, backwaters. |
| • Water depth | Shallow. |
| • Diet | Small fish e.g. minnow, bullhead, stickleback. |
| • Water chemistry | Sensitive to pollution. |
| • Bank slope | Vertical or overhanging bank (not undermined) above summer high water level. |
| • Soil type | Soft earth or compacted sand. |

- Terrestrial vegetation Dense trees and shrubs.
- Nest sites Bankside or upturned root plates.
- Perch sites Low, overhanging branches (≤ 2 m above water)
- Territory size Minimum nest spacing 0.3-1.0 km

6.1.2 Introduction

The kingfisher (*Alcedo atthis*) is a distinctive resident of British watercourses, lakes and coastlands. It is recognisable by its iridescent blue-green upper plumage, orange cheeks and underparts, small but stocky build (length approximately 16.5 cm), and its long bill (Boag 1982). Male and female adults are of similar appearance; except the lower mandible of the hen bird is rose-coloured.

The species' colloquial name is evidence of its perceived success as a riverine predator. This reputation has in the past led to persecution by fishermen and fish farmers who would set traps and block up the bankside nesting holes. The feathers were also used in tying flies for fishing, as ornaments and in millinery. Dr. W. Collinge highlighted misconceptions about the kingfisher's habits in 1921, in an attempt to improve the bird's reputation amongst anglers. Given that breeding ponds are secured against predation with fine mesh, the presence of the kingfisher may be advantageous, since it removes many of the predators of game fish ova (Eastman 1969).

The Protection of Birds Act (1954) provided legal protection for the kingfisher and under the Wildlife and Countryside Act (1981) it is now illegal to dig out the riverbank nest system of the kingfisher (Raven 1986). A more holistic approach is essential to halt the contemporary decline of populations, related mainly to pollution and territory loss.

6.1.3 Site Selection

Kingfishers choose to live within close proximity to their food source both during the breeding season and over winter. Their nests are most commonly built within the bank of a stream or tributary; less frequently alongside ditches, canals, reservoir embankments, banks of drowned gravel pits, lakes and farmland pools. The upturned rootplates of fallen trees may be important nesting sites locally (Riviere 1933). Other recorded sites include a rotten tree stump, a hole in a wall, a concrete tunnel and within a bank of a canal (Morgan and Glue 1977); banks of lanes and in clefts of caves (Eastman 1969). Observations of the bird in its natural environment have been used to further evaluate habitat suitability.

An overhanging (or vertical) bank of relatively soft earth or sand is generally preferred, sufficiently elevated to reduce risk of inundation by spring spates. Although banks of softer substrates are more commonly selected, harder sand, clay or earth strewn with flint nodules may be excavated successfully – the route of the burrow need not be straight (Morgan and Glue 1977). The density of riparian vegetation and the quality of the fishing may also be evaluated in site selection. Natural breaks in the river such as bays, stream junctions, river bends and backwaters may be favoured locally. Eastman (1969) noted avoidance of banks undermined by the burrows of water vole, although Morgan and Glue (1977) suggested that such burrows are occasionally enlarged and occupied by the kingfisher. Proximity to human habitation does not deter the kingfisher from nesting (Kumari 1978).

Keller *et al.* (1982) attempted to classify winter habitats of the kingfisher, listing five categories in order of apparent preference:

1. Very poor – water heavily polluted, bank drained and bare of shrubs and trees.
2. Poor – water unclear, banks drained and overgrown with low, herbaceous vegetation only.
3. Medium quality – water clear, river flowing through low meadows, scattered riparian trees or bushes.
4. Good – water clear, banks high (up to 2 m), trees and shrubs on both sides.
5. Very Good – water clear, trees and shrubs on either side, rich riparian vegetation, river connected with fish ponds by hatches.

6.1.4 Territory

There are many references to the behaviour of kingfishers during intra-specific conflict over territory (Clancey 1935, Eastman 1969, Kumari 1978, Keller *et al.* 1982), but records of interspecific competition are not so clear. It would appear from Kumari's (1978) account that a greater tolerance is displayed towards other species nesting within territorial boundaries: examples of robin, wren, sand martin and dipper are mentioned briefly. Clancey (1935) described attacks by kingfisher pairs on chaffinch, wren, dipper and sandpiper which suggest otherwise.

Territoriality commences soon after fledging and the young kingfishers no longer fish together, instead defending their favoured fishing sites. Two to three days after leaving the nest, almost all the young have departed from the parental territory and are otherwise treated as intruders (Clancey 1935). Intra-specific competition between dispersing juveniles may be suppressed to allow co-operative wintering of siblings. Keller *et al.* (1982) suggested that group tactics tend to be restricted to areas offering abundant available nest sites and during mild winters; in adverse conditions, siblings may be forced to separate in search of scarce resources.

Separate fishing territories exist within the otherwise joint territory of a pair, defended individually in the winter months when the pair no longer fish together (Eastman 1969). At the beginning of autumn, territoriality and aggression between individuals increases. Eastman observed the relocation of the cock bird (following the departure of the fledglings) to his part of the shared territory in early September, 1964 on the River Test.

The actual size of the individual or joint territory is unclear. Kumari (1978) found that territory length was 0.3-1.0 km for a population that had reached capacity (15 pairs along an 18 km section of the Ahja River, Estonia). In a population of reasonably spaced pairs, the majority of the fishing for the brood occurred at a distance up to several hundred metres from the nest, with little attention to territory. Favoured fishing spots develop within a territory, often with low, overhanging branches – it is rare for a bird to select food items from a distance exceeding 2 metres (Kumari 1978). However, should overcrowding occur then frequent conflict results and favourite sites are strongly defended. During severe conditions, when competition is at a maximum, a rival pair of intruding kingfishers may destroy the eggs and nest of the resident pair before establishing their own territory (Brown 1935).

6.1.5 Breeding

Having located a suitable bank, the kingfisher may engage in courtship flight-displays as early as December (although this usually takes place later) and on pairing, begin to excavate the nesting hole in mid- to late February (Eastman 1969). This is carried out by both birds

although it is the male that initiates nesting activity. Several tunnels may be started and rejected. The hole is usually excavated within 0-5 m of the banktop and leads into a bulbous nesting chamber through an inclined tunnel most frequently measuring between 31-90 cm. The length and profile may be partly determined by the nature of the bank material: see Figure 6.2 and Figure 6.3.

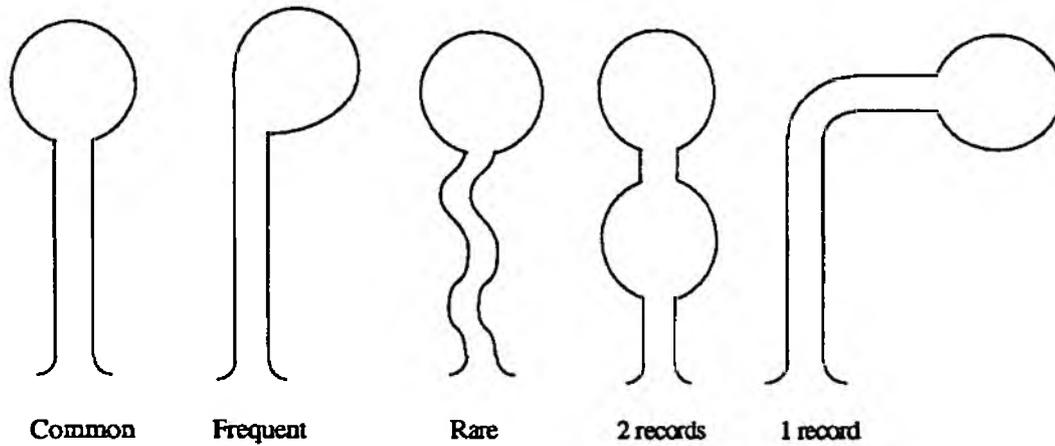


Figure 6.2 Kingfisher nest hole topography from above (Clancey 1935)

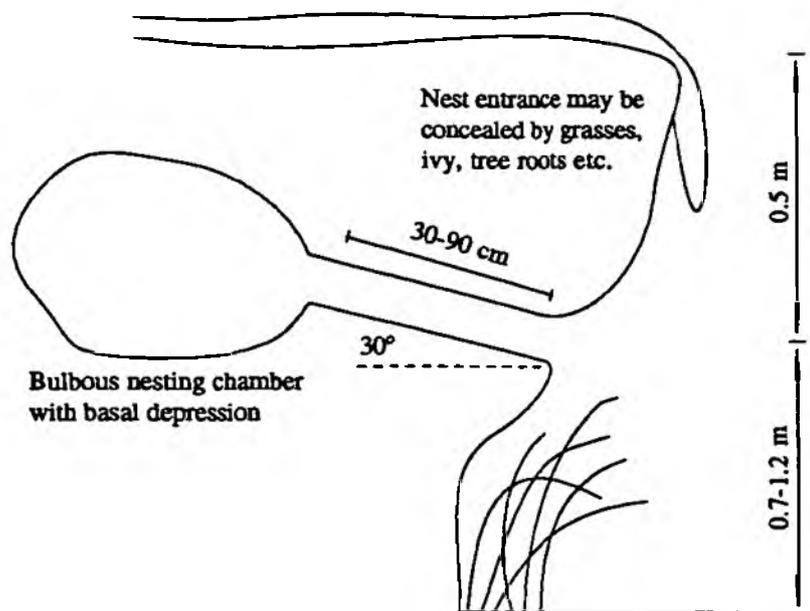


Figure 6.3 Section of typical kingfisher nest (measurements: Morgan and Glue 1977)

Areas offering extensive stretches of suitable bank may be returned to each year although the same hole is rarely used in consecutive seasons (Clancey 1935, Morgan and Glue 1977).

The kingfisher has a long breeding season. The first clutch is laid between the beginning of March and late July (Morgan and Glue 1977), the majority of breeding pairs making their first attempt in April. Kumari (1978) suggested that older pairs nest at an earlier date and attempt more clutches than the young birds that tend to nest later in the season. In response to

strong reproductive pressure (due to high mortality; see Section 6.1.8), the kingfisher commonly attempts two or three broods. The average clutch size is seven, most of which develop into nestlings (Clancey 1935, Morgan and Glue 1977, Kumari 1978). Following a successful brood it is likely that either the same nesting hole will be used for the second clutch or another will be excavated nearby. The second hole may be dug, clutch laid and incubation begun prior to fledging of the first brood (Brown 1935, Eastman 1969).

The pair take turns to incubate the eggs, changing places at about 1.5-hourly intervals, feeding and bathing between shifts (Eastman 1969). Single parents may, uncommonly, rear a brood with success (Kumari 1978). The incubation period is about 3 weeks; and the chicks remain in the nest for a further 4 weeks, moving into the tunnel after 10 days (Riviere 1933, Eastman 1969, Kumari 1978, Raven 1986).

6.1.6 Diet

It has been suggested that the kingfisher's diet reflects the composition of resources occurring within its territory, exploiting the most readily available food source first (Eastman 1969, Raven 1986). Its inland diet is primarily small fish or fry; molluscs and shrimps in coastal areas; and occasionally aquatic invertebrates (especially dragonfly nymphs and adults). The diet of the kingfisher is limited by its basic method of feeding. Stoneloach shelter beneath large stones, emerging to forage on dull days and at night; and are therefore absent from the diet, despite being dominant in many shallow areas (Raven 1986).

Raven (1986) identified nine fish species present in three yearly bone samples from two nests on the River Roding, Essex (Table 6.1). Minnow was the most abundant and the 3-spined stickleback was also prominent; of the other 7 species, none exceeded 5% frequency in any of the samples. Minnows are a reliable source of food for breeding kingfishers as they are most active during the day, and occur in large shoals for several weeks during spawning (Meadows 1972).

Table 6.1 Fish less than 100 mm length in a riffle habitat and the fish diet of young kingfishers in the same area (Raven 1986)

	% biomass in riffle		% of diet
	Total	Excl. stoneloach	
Chub <i>Leuciscus cephalus</i>	0.4	1.0	0.0
Dace <i>Leuciscus leuciscus</i>	0.3	0.8	2.6
Roach <i>Rutilus rutilus</i>	0.1	0.3	0.9
Gudgeon <i>Gobio gobio</i>	0.1	0.3	1.9
Minnow <i>Phoxinus phoxinus</i>	28.4	71.2	67.2
Goldfish <i>Carassius auratus</i>	0.0	0.0	0.1
Tench <i>Tinca tinca</i>	0.0	0.0	0.1
Bullhead <i>Cottus gobio</i>	0.5	1.3	0.0
Stoneloach <i>Neomacheilus barbatulus</i>	60.1	0.0	0.0
3-spined stickleback <i>Gasterosteus aculeatus</i>	10.0	24.5	27.0
10-spined stickleback <i>Pungitius pungitius</i>	0.2	0.5	0.0
Perch <i>Perca fluviatilis</i>	0.0	0.0	0.1
Pike <i>Esox lucius</i>	0.0	0.0	0.1

Adults select the size of the fish offered to young birds, increasing the length of the fish with the age of the brood (Riviere 1933, Raven 1986). The unfledged nestlings arrange themselves radially in the bulbous chamber with their beaks pointing outwards. The bird

closest to the tunnel waits to be fed, then ejects its faeces up to 30 cm along the tunnel; the group then rotates (Kumari 1978). Whilst in the nest the chicks receive fish 10-30 mm long, after which they normally feed in the tunnel and take larger fish about 50 mm in length (Raven 1986). The adults continue to feed the juveniles for several days near the nest, while the young birds will learn to fish for themselves in readiness for dispersal.

6.1.7 Migration

Generally, the British kingfisher has not been known to migrate over distances as far as those travelled by its continental relatives. Movements to the coast and river estuaries are influenced by the severity of climatic conditions in the winter months and the scarcity of food reserves. Some resort to garden ponds and there are records, during a particularly hard winter, of one bird attempting to swallow a shrew and another taking suet from a bird table (Eastman 1969). Individuals which migrate to coastal regions may also have to adapt their diet; shrimps and crustaceans then form a dominant component.

6.1.8 Mortality

Kingfishers lay clutches of 6-7 eggs and most attempt 2 broods per season. Since 62% of the nests succeed and 25% of young survive to breed, the average number surviving for each pair is about 1.5 (Morgan and Glue 1977). Kingfishers are therefore able to respond fairly promptly to improved conditions.

During incubation, human disturbance (including taking eggs, enlarging tunnels) accounts for the majority of failures. The kingfisher is particularly susceptible to engineering of lowland rivers; its prolonged breeding season means that the nest is at risk for 7 months of the year. Bank grading to improve capacity may completely destroy a site. Removal of bankside vegetation and of overhanging branches may also damage nests.

Intra-specific territorial conflict may result in damage of nests belonging to rival pairs and the eviction of eggs or nestlings from the chamber (Brown 1935). Repeated disputes can cause the adult pair to neglect their brood, which die of starvation or exposure (Eastman 1969). Peak mortality within the juvenile population occurs in August and September. After leaving the parental territory the young are inexperienced; and fall prey to water-logging and exposure, from constant wetting of the plumage (Eastman 1969, Morgan and Glue 1977).

Mortality amongst adult kingfishers is high, with a quarter of the population dying each year. Much of this occurs around January, when severe weather prevents fishing; and in April, at the beginning of the breeding season. High losses during the latter period are often associated with increased stress imposed by establishment and defence of territories. There are few natural predators of the kingfisher, with the exception of the domestic cat. The bird may have an unpleasant taste (Eastman 1969).

The kingfisher should not often be threatened directly, as a result of the 1954 Protection of Birds Act. Kingfishers feeds almost entirely on running water; and the distribution of breeding pairs shows an inverse relationship with stretches of grossly polluted rivers (Meadows 1972). Significant numbers of kingfishers have been re-colonising main river sites with a discharge exceeding 10 million gallons per day. Minnows can be up to 400 times more abundant in clear, shallow water of smaller tributaries but the main river has a greater capacity to dilute pollutants. Meadows (1972) found fish deaths from pollution more frequent and more extensive on smaller rivers; and concluded that the slower rate of kingfisher recruitment on small streams is related to their more fragile water quality.

6.2 Ducks

6.2.1 Habitat summary

Tufted duck (*Aythya fuligula*)

- Distribution See map (Figure 6.4)

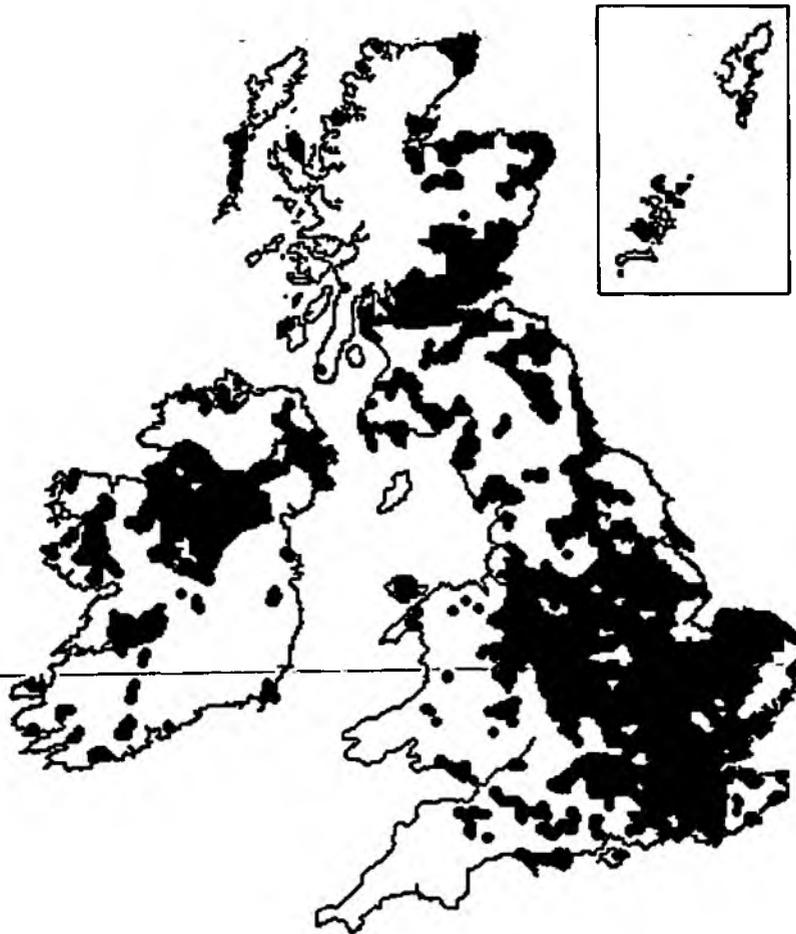


Figure 6.4 Broad distribution of the tufted duck in the British Isles (Sharrock 1976)

- | | |
|----------------------|---|
| • Flow regime | Lentic: lakes, reservoirs, park lakes, gravel pits. |
| • Topography | Islands. |
| • Altitude | Below 400 m above sea level. |
| • Geology | Limestone, non-acidic. |
| • Water depth | Deep, typically 3-5(-14) m |
| • Habitat size | At least 1 hectare |
| • Aquatic vegetation | Dense, emergent, up to 10 m breadth. |

- Diet Invertebrates, especially zebra mussel.
- Nest spacing 5-11m
- Associations Often with black-headed gulls.

Mallard (*Anas platyrhynchos*)

- Distribution See map (Figure 6.5): wet meadows, gravel pits.



Figure 6.5 Broad distribution of the mallard in the British Isles (Sharrock 1976)

- Altitude Lowland, but may be found up to 2000 m
- Topography Prefer islands.
- Water depth Shallow (< 1m)
- Flow rate Slow.
- Aquatic vegetation *Ranunculus*, *Glyceria*, marginal *Sparganium*.
- Terrestrial vegetation Dense, high: grass, nettles, brambles, bracken, heather.

- Nest sites First-year: nest on ground.
Second year: pollarded trees (e.g. willows), stumps and snags of large trees – diameter 48 cm (37.5-60 cm); elevation 1.8 m (0.46-4.6 m)
- Nest spacing At least 1 m

Mandarin duck (*Aix galericulata*)

- Distribution See map (Figure 6.6)

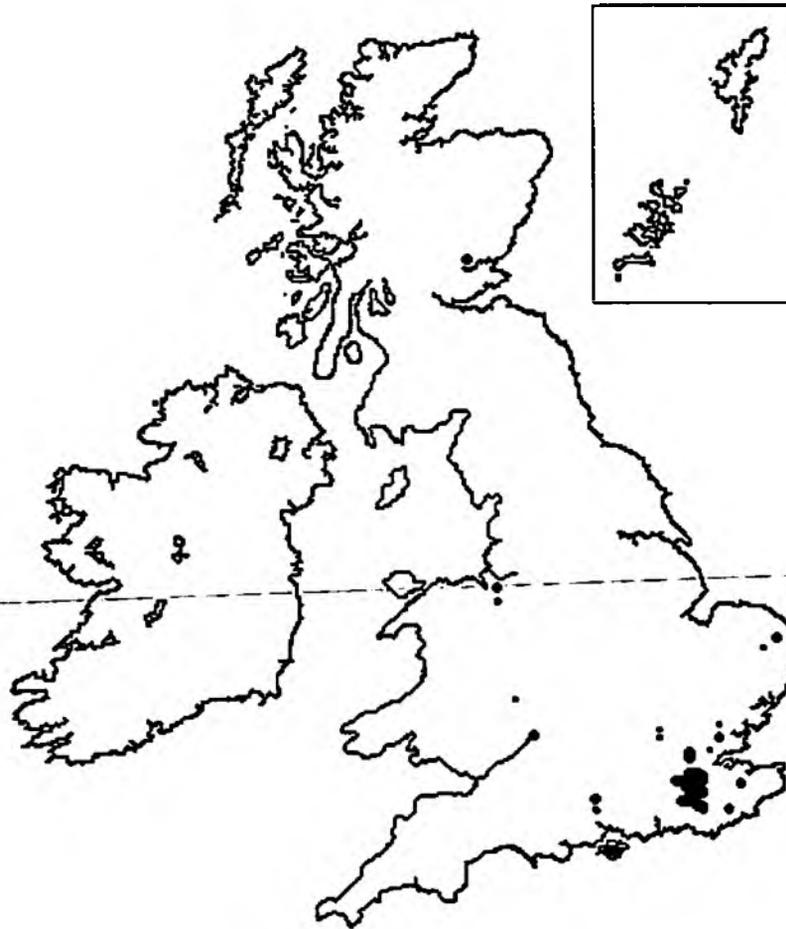


Figure 6.6 Broad distribution of the Mandarin duck in the British Isles (Sharrock 1976)

- Altitude ≤ 183 m above sea level.
- Aquatic vegetation Amphibious biotort.
- Nest sites Tree cavities, at least 0.5 m deep, 1.5-7.3 m above ground level, overhanging or close to water.
- Tree species First year: oak, ash.
Second year: sweet chestnut, beech, with cover.
- Nest-box dimensions 50.8 cm high; 20-25 cm wide and deep; entrance 10 cm \varnothing

Teal (*Anas crecca*)

- Distribution

See map (Figure 6.7): moorland pools, mires, bogs and braided streams.



Figure 6.7 Broad distribution of the teal in the British Isles (Sharrock 1976)

- | | |
|--------------------------|---|
| • Flow regime | Lentic, and lentic habitats on flowing waters. |
| • Chemistry | Prefer eutrophic conditions, acid-tolerant if food available. |
| • Altitude | Upland preferred. |
| • Aquatic vegetation | <i>Ranunculus</i> , <i>Eleocharis</i> . |
| • Terrestrial vegetation | Dense, more or less dry. |
| • Diet | Aquatic invertebrates in summer, vegetation in winter. |
| • Nest spacing | Minimum 1 m (not colonial) |

Pintail (*Anas acuta*)

- Distribution

See map (Figure 6.8): moorland pools, lochs and lowland lakes. Also freshwater marshes.



Figure 6.8 Broad distribution of the pintail in the British Isles (Sharrock 1976)

• Depth	Shallow, at least in margins.
• Terrestrial vegetation	Exposed, short grass.
• Diet	Omnivorous.
• Habitat size	50-200 m along waterside.
• Nest spacing	2-3 m (not colonial)

6.2.2 Predation

Many habitat studies of waterfowl have focussed on dietary and nesting requirements. Nesting work has emphasised the role of vegetative cover set against egg predation by species such as mink and crows (Rearden 1951). Opinion on the benefit of vegetation as a visual and olfactory barrier (Duebbert and Lokemoen 1976) has varied. There may even be no relationship between nest cover and clutch success when predators use indirect cues, such as hen movement, to locate nests (Schranck 1972). The greater relative success of late-season nesters (among taller vegetation) might be due to cover, but could also reflect increasing dietary choice of predators.

Predation on nests of gadwall was reduced in tall (>30 cm), dense vegetation (Sugden and Beyersbergen 1987). Dwernychuk and Boag (1972) found that egg loss from artificial nests by avian predation was inversely proportional to nest cover. This suggests that visual sighting of the nest is a key to avian predation. Additional cues must also be available: even when completely screened, the nests attracted 34% predation. Avian predators are probably deterred from seeking nests in cover because search effort is increased; and because vigilance is more difficult in respect of their own predators. Clutches are usually guarded and are not open to avian predation. Nest concealment may be most important during laying, when the eggs are most exposed and the female less attentive; and when adults are disturbed and forced to vacate the nest.

It seems likely that predator control (e.g. trapping, electric fences) should increase the clutch success of waterfowl (Greenwood *et al.* 1990). Schranck (1972) compared nesting success with vegetation density under controlled and uncontrolled predation (Table 6.2). In the case of artificial/simulated nests, control of predators increased overall nesting success, which was always higher with vegetative cover.

Table 6.2 Effect of predation and cover on waterfowl nesting success (Schranck 1972)

	Mean % success	% increase of success with vegetative cover
Natural nests	43	26
Simulated nests (no predator control)	46	35
Simulated nests (predator control)	72	44

Ducks prefer to nest on islands rather than mainland sites, reducing the incidence of mammalian predation (Sharrock 1976). Nests densities are typically about 40% higher on islands (Hill 1984).

6.2.3 Tufted duck (*Aythya fuligula*)

The tufted duck is one of our most successful breeding waterfowl. It generally nests near lakes and reservoirs, especially those containing islands; but a recent population increase has been attributed to use of urban park lakes and gravel pits. The main physical requirements of nesting are at least a hectare of water below 400 m altitude and basic geology (Sharrock 1976).

The nest of the tufted duck is generally found on dry ground, less than 10 m from the water and hidden by emergent vegetation. Occasionally, nests are found over water on reed platforms or in abandoned coot nests. The tufted duck may breed socially on islands: an island on Loch Leven holds 500-600 pairs, with an average spacing of 5-11 m between nests. Breeding success might be increased by breeding-site association with black-headed gulls, which readily deter predators. The nest depression is made by the female and is lined with grass, rushes, reed and down (20-25 cm diameter and 7-10 cm depth: Cramp *et al.* 1977). The tufted duck lays late in the year, from mid-May onwards and sometimes after July. The female incubates the eggs for 23-28 days and then cares for the brood until they fledge, 45-50 days after hatching (Cramp *et al.* 1977). The largest breeding concentrations are found at Lough Beg and Lough Neagh, 800-1000 pairs; Loch Leven, 500-600 pairs; and Lower Lough Erne, 200 pairs (Sharrock 1976).

The tufted duck is capable of dives reaching 3-14 m, and can thus colonise deeper waters (3-5 m preferred during breeding: Cramp *et al.* 1977). Its diet varies with season and locality.

In winter it is often predominantly carnivorous, with one staple English food being the zebra mussel. In the spring and summer, seeds become more important food sources.

6.2.4 Mallard (*Anas platyrhynchos*)

The mallard inhabits a wide range of water types (freshwater and marine) from small ponds to the open sea. Most usually it is found on shallow (<1 m) slow-flowing waters. The mallard prefers lowland sites, but may be found above 2000 m (Bauer and Glutz von Blotzheim 1968: cited by Cramp *et al.* 1977).

The mallard breeds about 5-6 weeks before the tufted duck (Sharrock 1976). Therefore the mallard nest is found in shorter, younger vegetation; in which it is more susceptible to predation. The early hatching of mallard chicks coincides with a peak of chironomids which are important in their diet. If the first nest is destroyed a second clutch of eggs can be produced; this is not the case with the later-breeding tufted duck, for which the clutch represents a greater energetic investment (67% versus 42% of body weight: Hill 1984).

Mallard nest density was found by Lokemon *et al.* (1990) to be greatest in habitats providing highest and densest nest cover. There was a significant relationship between nest density and a 'visual obstruction rating' (Table 6.3). Although usually associated with water, nests are sometimes made on hillsides distant from the water (Sharrock 1976: see Figure 6.9).

Table 6.3 'Visual obstruction rating' and mallard nest density (Lokemon *et al.* 1990)

	Stubble	Pasture	Hayland	Dry wetland	Canal	Odd areas *	Roadside	Seeded cover
Spring VOR	-	0.24	0.15	-	1.27	1.00	0.51	1.37
Summer VOR	-	1.25	2.80	-	3.80	3.25	3.20	4.11
Nests/km ² 1976-78	0.0	0.8	0.8	2.7	6.7	13.0	4.4	**
Nests/km ² 1979-81	1.1	5.1	6.9	35.6	44.3	43.4	48.5	60.6

* includes hedgerows, farmsteads, shelter-belts and rock piles ** none available

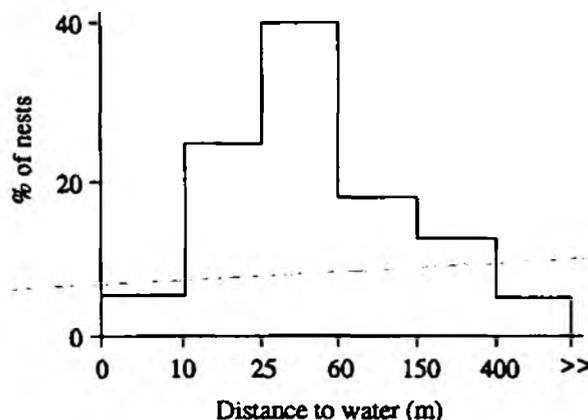


Figure 6.9 Distance of mallard nests from open water on Cors Fochno (Fox 1986)

The probability of a female mallard returning to a previous nesting site is proportional to her previous breeding success (Majewski and Beszterda 1990). Birds over two years old arrive significantly earlier at the breeding sites (Lokemon *et al.* 1990) and hence have first choice of habitat; but there is no evidence of age-relation in timing of the nesting itself.

Birds that have previously been unsuccessful tend to increase the distance between nests but there is no systematic effect of age on nest-spacing (Lokemon *et al.* 1990). Ducks nesting at higher densities take part in more interactions, leading to neglect of nest-guarding and increased egg predation (Hill 1984). This reduces the value of nestbox provision, unless predators are controlled. The most effective approach is to increase the area of suitable habitat.

Mallards require a source of protein-rich invertebrate food for reproductive success. Food quality affects egg size (down to 75%) more than clutch size, which only decreases in very severe conditions. This strategy was considered by Pehrsson (1991) in terms of the temporally variable nature of the wetland environment. Food limitations experienced by the mother (leading to lightweight eggs) might not be experienced later in the season by the chicks (their hatching coincides with chironomid abundance) and hence chicks from lightweight eggs may not be permanently disadvantaged.

Although the mallard is usually a ground-nester, individuals may be found nesting above ground level. Five percent of mallard nests in Decoy Wood, Slimbridge were found in the crowns of pollarded willows (cited by Bjärvall 1970). The most common natural sites for raised nests are stumps and snags of large trees where the bole has broken off leaving a cup-shaped depression (Cowardin *et al.* 1967). These nests are generally found above open water with floating aquatic vegetation. Success for tree-borne nests can be higher than for the conventional ground nest, due probably to reduced predation (Cowardin *et al.* 1967).

The mallard feeds by a number of methods (Cramp *et al.* 1977) both in the water and on land:

- Pecking and sieving, i.e. 'dabbling'
- Submerging head and neck and up-ending (Up to 48 cm for 4-8 seconds)
- Diving (depths 1-2 m, most common in juveniles)
- Grazing or picking up individual items with beak tip, sometimes shaking plants to loosen seeds and attached invertebrates.
- 'Grubbing' at the base of plants.
- Biting out pieces of larger food items (e.g. potatoes)

The list of food items recorded in the diet of the mallard is extensive (Table 6.4) but largely consists of immobile items in the size range 1-10 cm (Olney 1964).

Table 6.4 Food items of mallard (n=210) over 8 seasons, Sep-Jan in Kent (Olney 1967)

Wet Meadows	River banks
<i>Ranunculus repens</i> seeds	<i>Sparganium erectum</i> seeds
<i>Polygonum persicaria</i> seeds	<i>Polygonum hydropiper</i> seeds
<i>Carex hirta</i> seeds	Gravel Pits
<i>Rumex conglomeratus</i> seeds	<i>Alnus glutinosa</i> seeds
River	<i>Sparganium erectum</i> seeds
<i>Ranunculus aquatilis</i> leaves and stems	<i>Polygonum</i> spp. seeds
<i>Glyceria fluitans</i> seeds	<i>Equisetum</i> sp.
<i>Potamopyrgus jenkinsi</i>	<i>Chironomidae</i>
<i>Hydropsyche angustipennis</i>	<i>Hydropsyche</i> spp.
	<i>Quercus robur</i> seeds

6.2.5 Mandarin duck (*Aix galericulata*)

The Mandarin duck (*Aix galericulata*) was first introduced into Britain in 1745, although the present feral population originated in the first half of the 20th century. It was not until 1971 that this bird was included on the British and Irish lists of breeding birds. From 1745 to 1988, mandarin ducks have been recorded at more than 1000 British sites, in 397 10-km squares (Davies 1988). This duck is mainly found in south east England, with the only northern population on the River Tay (Davies 1988). The drakes have a sombre 'eclipse' plumage from May until September, after which they moult and produce their display plumage (Savage 1952).

Mandarins form monogamous pairs, which may continue for more than one season. They exhibit a strong homing instinct; older females arrive and lay earliest, often reclaiming old nest sites. These ducks are more arboreal than our native species, with a great deal of manoeuvrability whilst in flight; individuals tend to fly below the canopy weaving amongst the trees (Sharrock 1976). Mandarin ducks generally breed in tree cavities which are more than 0.5 m deep. Most nests are found between 1.5 and 7.3 m above ground level, as far as 3.4 m from the entrance hole (Davies 1985). Cavities in oak and ash trees contribute 75% of recorded nest sites (Davies 1985, Davies and Baggott 1989). Nests are also found in sweet chestnut and beech trees which can provide a winter diet of nuts and seeds (Sharrock 1976). There is some requirement for supplementary cover such as rhododendron thicket.

Davies (1985) found that 87% of Mandarin nests were located on cultivated or maintained land, with 10% of the remaining nests being found in woodlands (both deciduous and coniferous). The majority of nests are found near water and at less than 200 m altitude, although in Japan, their place of origin, they have been recorded at altitudes up to 610 m.

The Mandarin duck can be induced to use nest-boxes, which can then be successfully lowered to a level more convenient for ringing and observation. This practice is particularly useful where current management techniques have removed standing old wood from an area. Davies (1985) recommended the nestbox dimensions shown in Figure 6.10.

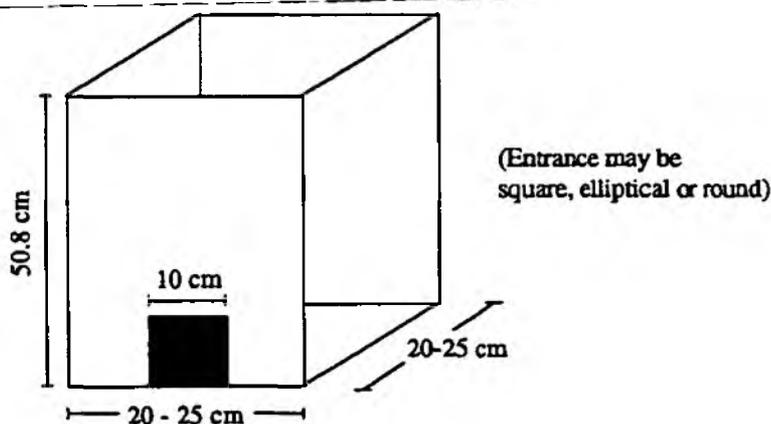


Figure 6.10 A typical nest-box design for the Mandarin duck. (Davies 1985)

The eggs are laid from March until late June, and clutch replacement is common in cases of initial failure. A single nest site being can be used successively in the same season by different females. The modal clutch size is 9-12 eggs; but one study found most clutches in excess of this figure (Davies and Baggott 1989). Clutch size variability has been attributed to intra-specific nest parasitism ('dump nesting' of eggs by females other than the incubator).

This phenomenon is not caused by a lack of available nest sites. It appears that artificial nest-sites tend to bear smaller clutches (Davies *et al.* 1989), perhaps suggesting they are less susceptible to nest parasitism.

Incubation lasts for 28-30 days. Emerging chicks claw their way up the sides of the nest chamber and can then drop safely to ground level due to their lightness and thick down. The hatchlings take 40-45 days to fledge, after which they are independent (Cramp *et al.* 1977).

Mandarin ducks are omnivorous, mainly eating vegetable matter which it supplements with some invertebrates. They may feed at any time, on land or whilst afloat, though they rarely dive for food. The diet has a degree of seasonality but there is little detailed information. The autumn/winter diet of the British population largely consists of nuts – acorns, chestnuts (*Castanea* or *Aesculus*) and beechmast (Savage 1952). In the summer, the ducks frequently take insects from the surface of the water and from aquatic plants (often amphibious bistor: Savage 1952).

Holes which appear suitable for tawny owl, little owl or kestrel nests are likely sites for the nests of Mandarin ducks, especially where these are close to (Davies 1985), whilst in the unusual case of a shallow nest cavity it may be possible to see white down in the chamber (Sharrock 1976). Current estimates regarding the size of the British Mandarin duck population are probably low, due to the difficulties of surveying such elusive, secretive birds. In 1985 the collection of BTO Nest Records for this species amounted to 134 cards which had been submitted by only 19 observers (in 7 areas of Britain). Davies (1988) extrapolated survey data to produce a more realistic population estimate of more 7000 birds (far greater than previous figures). Based upon this work, the British population would form about 1/3 of the world total, outranking the Japanese population and the remaining Asian populations outside Japan - the British stock is therefore of global importance.

6.2.6 Teal (*Anas crecca*)

In Britain, teal prefer moorland pools, bogs and braided rivers – especially upland waters. The greatest numbers are found in the north and west of the country, though a substantial population does exist in the south. Teal are found on most water systems except those that are very deep, fast-flowing or exposed (Cramp *et al.* 1977). There are few on the western coast of Scotland, possibly due to the wet summer weather in this region and/or its sparse vegetation (Sharrock 1976). Lowland communities are infrequent and only occur when cover is available from emergent and marginal vegetation. The teal tends to favour eutrophic waters, although if sufficient food is available, it can tolerate neutral or partially acidic conditions (Cramp *et al.* 1977). Teal will breed in patches of bog which contain standing water, especially near ditches which hold water throughout the summer months.

Monogamous pairs are formed during the breeding season. Nests are generally slight hollows formed at ground level amidst thick cover such as tussocks or overhanging bushes. Nests may exceptionally be found as close as 1 m apart but usually pairs are more or less solitary (Cramp *et al.* 1977). Incubation, by the female, starts in late June-July and lasts for 20-22 days, with the nest being covered with down whenever the female is away (Sharrock 1976, Cramp *et al.* 1977, Fox 1986). The female and young tend to remain well-hidden, making population surveys difficult. It is not viable to correlate sightings of males to the local breeding population, because drakes abandon the females at the start of incubation.

The teal tends to be more closely associated with water than the mallard, both in its nest location and in the movement of pre-fledging broods (see Figures 6.11 and 6.12). The level of duckling mortality increases with the distance from nest to nursery feeding area. Fledging occurs 25-30 days after hatching (Cramp *et al.* 1977).

Cors Fochno (Borth Bog, part of Dyfi National Nature Reserve; Fox 1986) is a coastal peatland complex whose undamaged raised mire vegetation is surrounded by a zone of drained bog. Management in the 1980s at Cors Fochno aimed to restore peatland and flora by blocking up drainage ditches - these works have proved beneficial to the teal populations. There has been an increase in the density of Odonata, reflecting a general increase in invertebrate numbers. Invertebrates form 80-90% of the diet of young teal between hatching and 14 days (Fox 1986).

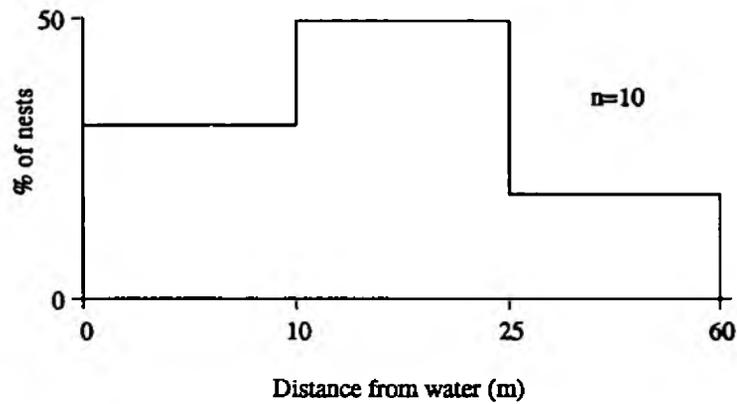


Figure 6.11 Separation of teal nests from open water on Cors Fochno (Fox 1986)

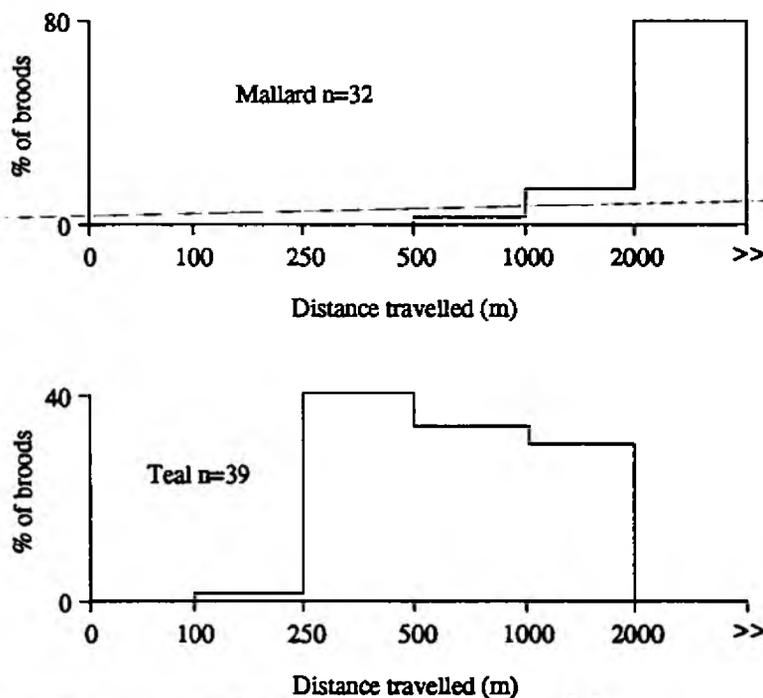


Figure 6.12 Comparison of movement by mallard and teal broods from first sighting to the last sighting before fledging and dispersal (Cors Fochno; Fox 1986)

The teal is omnivorous but its diet changes seasonally: animal matter (up to 11 mm) predominates in the spring/summer; and seeds (1-2.6 mm) in the autumn/winter. Olney (1963)

identified 66 plants species in the stomach contents of 96 birds during September-January, comprising 83.6% of total volume. The main constituents were seeds of *Eleocharis palustris* and *Ranunculus repens*. Their food requirement is 20-30 g (fresh weight) per day, towards which they use several feeding techniques (Cramp *et al.* 1977):

- In shallow water, filtration of of small seeds from fine mud.
- Swimming with head (and sometimes neck) submerged.
- Up-ending.
- Picking items off the surface of the water or associated plants.
- Skimming surface of water with the bill (occasional)
- Diving (rare)

The Teal uses breeding sites on a very sporadic basis, possibly using a given site only once or twice in ten years. Hand-rearing is difficult, so there is little supplement of wild stocks with captive-bred animals. A 1968-72 field survey in central and northern Scotland, Ireland and eastern England suggested a British population of 3500-6000 pairs (Sharrock 1976).

6.2.7 Pintail (*Anas acuta*)

The pintail (*Anas acuta*) was first shown to breed in Scotland in 1869; in England in 1910; and in Ireland in 1917 (Sharrock 1976). It is a dabbling duck and requires waters which are shallow (at least at their periphery). It prefers large open waters and is seldom found on narrow waters supporting dense aquatic vegetation or bordered by forest.

Pintail nest by moorland pools, lochs and lowland lakes, as well as on freshwater marshes. Nests are usually exposed on short grass and situated 50-200 m from the water (Sharrock 1976). The pintail is not a colonial nester, but nest spacing may be 2-3 m (Cramp *et al.* 1977). The female forms a slight hollow which is lined with down. Each female raises a single brood per season although clutch replacement is possible. The eggs are incubated by the female for 22-24 days, and the young fledge and are independent 40-45 days after hatching.

Feeding is usually nocturnal, on a wide variety of plant and animal matter (Cramp *et al.* 1977: see Table 6.5). The main feeding technique is by up-ending to probe fine substrata, but less commonly the pintail may dive for food or may forage on land (eating seeds and digging up rhizomes and tubers).

Table 6.5 Food items of pintail (Cramp *et al.* 1977)

PLANTS		ANIMALS	
<i>Potamogeton</i>	<i>Pilularia</i>	Coleoptera	Hirudinea
<i>Elodea</i>	<i>Spergularia</i>	Diptera	<i>Artemia</i>
<i>Vallisneria</i>	<i>Ceratophyllum</i>	Trichoptera	Copepoda
<i>Carex</i>	<i>Zostera</i>	Odonata	Phyllopora
<i>Rumex</i>	<i>Chara</i>	Orthoptera	Ostracoda
<i>Polygonum</i>	Algae	<i>Hydrobia</i>	Amphibian tadpoles
<i>Glyceria</i>	Cereals, rice and potatoes	<i>Planorbis</i>	Fry

6.3 Swans

6.3.1 Habitat summary

Mute swan (*Cygnus olor*)

- Distribution See map (Figure 6.13): lentic and lotic.



Figure 6.13 Broad distribution of the mute swan in the British Isles (Sharrock 1976)

- Flow rate Slow or still.
- Altitude Below 300 m above sea level.
- Aquatic vegetation Submerged e.g. *Ranunculus*, *Potamogeton*.
- Open water Sufficient for unwieldy take-off.
- Nest form Large mound: height 60-80 cm, basal width 1-2 m
- Nest spacing Mean 2-4-3-2 km, minimum 90 m
- Pollution Tolerant, possibly prefers eutrophication.

Bewick swan (*Cygnus columbianus*)

- Distribution Non-breeding: flooded grasslands, lotic and lentic.
- Altitude Lowland, below 100 m above sea level.
- Marginal vegetation First year: *Glyceria fluitans*, *Agrostis solonifera*, *Alopecurus geniculatus*, *Trifolium repens*.
Second year: *Glyceria maxima*, *Rorippa palustre*.
- Disturbance Sensitive.

Whooper swan (*Cygnus cygnus*)

- Distribution Non-breeding: freshwater and marine habitats.
- Marginal vegetation *Rorippa palustre*, *Equisetum*, *Glyceria*.
- Terrestrial vegetation Stubble and arable crops.

6.3.2 Mute Swan (*Cygnus olor*)

The mute swan is an indigenous bird which was semi-domesticated in medieval times for culinary purposes. Over the past 200-300 years *C. olor* has returned to its wild state; although it remains tolerant of disturbance. In 1955, a BTO survey of mute swans in England and Wales logged 14 300 - 15 300 birds, including 3000-3500 breeding pairs (Sharrock 1976). Swans are often associated with slow-flowing waters; but their main requirements are submerged vegetation, and enough space in the channel to take flight. In 1986, 94% of our mute swans were associated with inland waters (Sears 1989). Lentic and lotic habitats are both used (Eltringham 1963: see Table 6.6). Breeding pairs of mute swans are not generally found more than 300 m above sea level.

Table 6.6 Distribution of mute swan nests according to habitat (Eltringham 1963)

Habitat type	Nests	Habitat type	Nests
Standing water (46%)	467	Moving water (49%)	499
Lakes and ponds etc	287	Rivers	346
- in urban parks	50	Canals	63
- lakes	88	Drains	90
- ponds	110	Coastal (5%)	47
- broads	15	Estuarine	11
- mill ponds	24	Saltmarsh	25
Flooded pits	116	Seashore	3
Reservoirs	50	Freshwater lagoon	8
Miscellaneous	14		

The mute swan begins to nest in the early spring, laying from March onwards. Many of the young are fully grown by late August. The nest consists of a mound of fresh and dead plant material (e.g. rushes, reeds) within 100 m of the water. Nest construction takes about 10 days with the male generally collecting materials which the female places and shapes (Cramp *et al.* 1977: see Figure 6.14). Nests may be slightly less distinct when built on vegetated islets or in reed beds but are revealed by aggressive territoriality of the cob (male).

Soft vegetation and down line the depression.

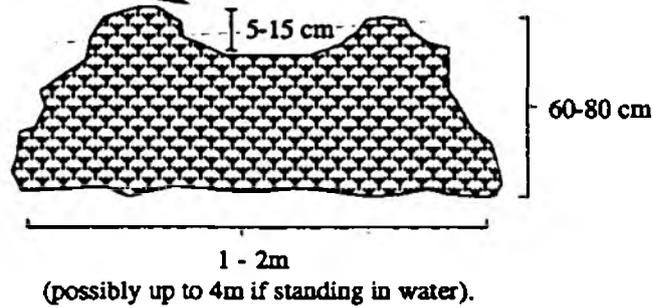


Figure 6.14 Typical dimensions of mute swan nest.

A single clutch of about 6 eggs is most common (Perrins and Reynolds 1967, Cramp *et al.* 1977, see Figure 6.15) in swans of all ages. Clutch replacement is possible within 2-4 weeks of a loss, though with fewer eggs (Cramp *et al.* 1977). Incubation, mainly by the female, takes 36 days. More than 25% of the weight of new hatchlings is formed by the yolk sac, which is retained within the body cavity and can provide sufficient nourishment to sustain the bird for several days (Reynolds 1965: cited by Perrins and Reynolds 1967). Cygnets experience about 30-50% mortality, with a modal spring brood size of 4 (Eltringham 1963: see Figure 6.16) and autumnal mean brood of 3.1 (Reynolds 1965). The parent birds both care for the cygnets, with the female often carrying the young during the first 10 days (and sporadically for the next 6 weeks: Cramp *et al.* 1977). Fledging takes 120-150 days, and many of the young are forced to disperse in autumn due to the territoriality of the parent birds. The young then join non-breeding flocks. Plumage changes from dark brown to white with maturation; immatures also have a lead-coloured bill which becomes red. The territories of the mute swan are typically 2.4-3.2 km, though exceptionally nest-spacing can be 90 m (Perrins and Reynolds 1967).

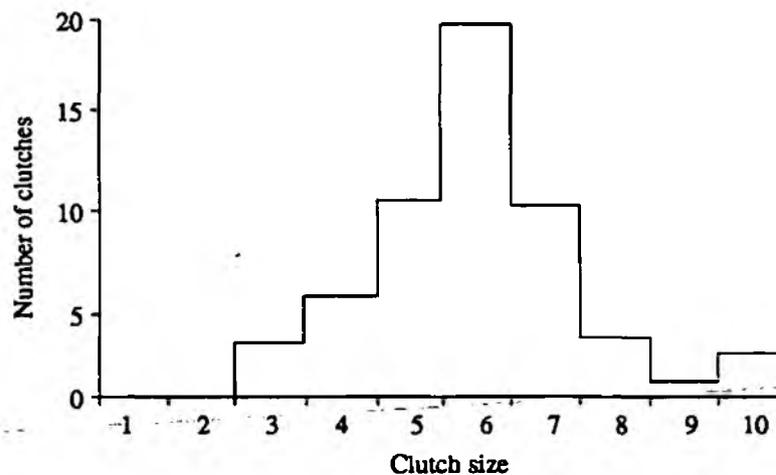


Figure 6.15 Clutch size of the mute swan (Eltringham 1963)

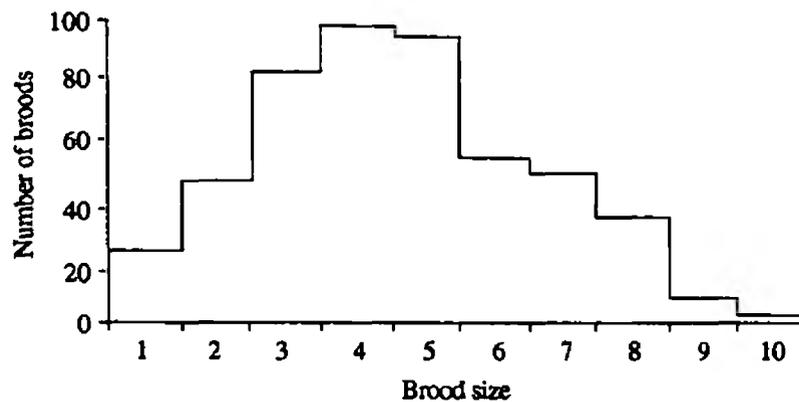


Figure 6.16 Spring brood size of the mute swan (Eltringham 1963). Most broods were recorded in May or early June when the cygnets were probably under one month old.

An important component of the diet is submerged aquatic vegetation (e.g. *Ranunculus*, *Potamogeton*) of which it consumes about 4 kg per day. These are obtained with head and neck submerged for about 10-13 seconds in water of 20-100 cm depth (Cramp *et al.* 1977). The swan is, however, an opportunistic feeder and may be found eating a wide variety of vegetable items (e.g. wheat, grass, bread). Cereals and coarse grasses have a high fibre content (wheat 37% dry matter *cf* 14% for submerged aquatics) rendering them relatively indigestible by swans, which require a larger daily intake of such food (Sears 1989). Mute swans also expend more effort when feeding on land, since they drop a large percentage of vegetation cropped.

The mute swan is fairly tolerant of pollution, except oil and toxic chemicals. It may benefit from the enhanced plant growth associated with eutrophication. A major cause of swan mortality has been lead poisoning from ingestion of shotgun pellets and anglers' lost/discarded shot. Locally, up to 94% of swan deaths have been lead-related (Sears 1988). Lead poisoning can be fatal directly or through impairment of the nervous system (Birkhead and Perrins 1985, O'Halloran and Myers 1989).

6.3.3 Whooper swan (*Cygnus cygnus*)

The whooper swan does not breed in Britain; but winters in flocks along marine and freshwater systems (e.g. the coast, chains of lakes and rivers). It often walks and can be distinguished from the mute swan by its straight, stiff neck when swimming.

The preferred diet is the leaves, stems and roots of aquatic vegetation but if necessary the whooper swan will forage amongst fields of stubble and arable crops (even potatoes). A whooper swan stomach (taken from East Anglia) contained 90% (by weight) of the roots and crowns of marsh yellow-cress (*Rorippa palustre*), along with the shoots and leaves of horsetail (*Equisetum* sp.) and grasses (*Glyceria* sp.) (Cramp *et al.* 1977).

The whooper swan is sensitive to human disturbance but only displays limited aggression towards other swan species.

6.3.4 Bewick Swan (*Cygnus columbianus*)

The Bewick swan breeds in the Arctic but it has wintered in Britain at least since the 1930s. It prefers lowland sites below 100 m in areas which are undisturbed and have associated flooded grasslands, providing suitable grazing (e.g. lakes, pools, reservoirs and

ivers). Bewick swans tend to return to regular sites although their flight pattern may change over a period of about a decade.

During its stay the Bewick swan is a gregarious bird which feeds upon leaves, roots, shoots, rhizomes and tubers. One dietary study at the Ouse-Washes, suggested that this bird prefers to eat soft plants such as *Glyceria fluitans*, *Agrostis stolonifera*, *Alopecurus geniculatus* and *Trifolium repens*; and it will also eat coarser species such as *Glyceria maxima* and *Rorippa palustre* in winter or during deep flooding (Cramp *et al.* 1977).

Following a mild winter, the Bewick swan will return to its breeding grounds in early February but they usually remain in Britain until early March.

6.4 Coot (*Fulica atra*)

6.4.1 Habitat summary

- Distribution See map (Figure 6.17)



Figure 6.17 Broad distribution of the coot in the British Isles (Sharrock 1976)

• Altitude	Up to 500 m above sea level but absent from some areas above 230 m (e.g. Pennines, Wicklow and Mourne Mountains)
• Depth	Shallow.
• Flow rate	Slow or still.
• Nutrient status	Eutrophic.
• Aquatic vegetation	Submerged.
• Habitat size	At least 0.5 hectares.
• Terrestrial vegetation	Collapsed <i>Phragmites</i> and coarse woody debris.
• Diet	Predominantly vegetation.

6.4.2 Site selection

The coot uses a fairly narrow range of habitats, and this specificity combined with its size and conspicuous, gregarious, behaviour allows accurate population surveys. Lentic or slow-flowing waters are favoured but coot may also breed on lakes, areas of landlocked sea, and reed-fringed drainage dykes of coastal marshlands. The coot usually chooses areas of water over 0.5 ha for breeding (Sharrock 1976) and in recent years, disused sand/gravel pits have provided a new habitat. Unlike other Rallidae, the coot does not show a strong association with cover (in the water or on land) and groups are often seen on exposed banks or grassy fields close to the waters' edge (Cramp *et al.* 1980).

6.4.3 Breeding

The stone-coloured, speckled eggs are found in clutches of 4-8 in fairly open nest sites. They are often taken by crows: incubation begins before the clutch is complete, reducing the time that the eggs are vulnerable. The male and female both incubate the eggs, providing a continuous guard for the nest. The coot is aggressively territorial throughout the breeding season (Cavé and Visser 1985, Cavé *et al.* 1989) and often attacks other species (Salathé 1987). In the event of egg loss, clutch replacement may occur and may be at an alternative nest site.

Coot nests are often constructed using collapsed reeds or fallen branches for support and cover. It appears that there is a selective advantage between potential nest sites based upon their vegetation type format (Salathé 1987). Nests are most successful in dense *Phragmites* beds and least so in open beds of *Typha* or *Schoenoplectus*. The tamarisk tree, an introduction mainly to the south of England, has been used with intermediate success. Within a habitat plot, there appears to be no selectivity between plots of different cover density (Salathé 1987). Proximity to water is a more important influence on nest choice, than is the vegetation cover.

6.4.4 Diet

The coot is mainly a herbivorous bottom feeder, diving for submerged vegetation which it eats at the water surface (Cavé and Visser 1985). Cramp *et al.* (1980) found that the average content of 157 coot stomachs was 84.1% plant material and 15.9% animal matter (see Table 6.7). The foraging dives of the coot do not generally go deeper than 2 m, although there are records of 7 m dives (Sharrock 1976); and for this reason the coot favours shallow, eutrophic waters. In the restricted food availability of winter, coot may graze on adjacent grassland (Sharrock 1976, Odin 1988).

Table 6.7 Food items of coot (Cramp *et al.* 1980)

ALGAE	HIGHER PLANTS		ANIMALS
<i>Chara</i>	<i>Potamogeton</i>	<i>Myriophyllum</i>	Mollusca
<i>Vaucheria</i>	<i>Zarnichellia</i>	<i>Najas</i>	Insecta
<i>Cladophora</i>	<i>Zostera</i>	<i>Scirpus</i>	
<i>Spirogyra</i>	<i>Vallisneria</i>	<i>Phragmites</i>	
<i>Ectocarpus</i>	<i>Lemna</i>	<i>Phalaris</i>	
<i>Nostoc</i>	<i>Ceratophyllum</i>	<i>Typha</i>	
	<i>Ranunculus</i>	<i>Sparganium</i>	
	<i>Polygonum</i>	Terrestrial Graminaceae	

6.4.5 Range

The coot is absent from certain high land forms more than 230 m above sea level (e.g. Pennines, Wicklow and Mourne Mountains), but this restriction does not appear to be determined solely by altitude, since nesting at more than 500 m has been recorded in Scotland. It is probable that the lack of vegetation in the deep waters associated with particular uplands is the excluding factor.

6.5 Moorhen (*Gallinula chloropus*)

6.5.1 Habitat summary

- Distribution See map (Figure 6.18): lentic or lotic.
- Altitude Up to 600 m above sea level.
- Flow rate Broad tolerance.
- Aquatic vegetation — — — Emergent, e.g. *Carex acutiformis*, *Glyceria fluitans*.
- Diet Omnivorous.
- Disturbance Susceptible to human disturbance but tolerant of livestock.

6.5.2 Introduction

The moorhen (*Gallinula chloropus*) has a wide range of habitat preferences which encompass both lentic and lotic environments. Moorhen do not skulk amongst vegetation but display a preference for close vegetative cover when startled. They tend to breed less than 600 m above sea level and avoid fast flowing waters. Hence, the moorhen is absent from the Scottish highlands, the mountains of Kerry and central Wales and the higher parts of Dartmoor, Exmoor and Mayo (Sharrock 1976).

The moorhen is largely sedentary and may defend some form of territory throughout the year, although some individuals only hold territories from March until October/November, with common winter feeding grounds (Sharrock 1976). Varying degrees of territoriality are shown during the breeding season (Wood 1974), with territory size and quality reflecting the individual's ability to defend resources (Petrie 1984).



Figure 6.18 Broad distribution of the moorhen in the British Isles (Sharrock 1976)

6.5.3 Breeding

The moorhen begins egg-laying from mid-late March and continues into August. The usual clutch size has been cited as 7 eggs, while records of 13-20 egg clutches may be due to 'nest-dumping' which is quite common in moorhens. The ease of recording nest sites depends upon the time of their construction. Early season sites are more conspicuous due to the lack of cover from emergent vegetation.

The moorhen builds 3 types of structure for breeding purposes (Wood, 1974). Display platforms, used for sexual display and coition, are constructed from any available material during late February onwards. They are loosely constructed (durability *c.* 3 weeks), 2-5 cm deep with a diameter of 20-25 cm. There may be up to 5 display platforms within a single territory (Sharrock 1976). Egg nests are then constructed about a week before egg-laying, with collection and construction by the male and female respectively. Incubation, which usually last for 21-22 days, is shared. Most pairs build 2 nests during their first bout of breeding, one acting as a roost for the non-incubating parent. Replacement clutches are usually reared using a single nest. Brood nests are built quickly after the brood has hatched, sometimes taking less than 8 hours. The number of brood nests increases with the number of young.

The moorhen nests on water, or suspended above it, or on mud-banks which are surrounded by water, using emergent vegetation as cover. The external construction of egg nests is fairly rudimentary consisting of twigs and reed stems; but it is lined with finer materials

such as leaves. Where possible the moorhen builds using *Carex riparia/acutiformis* or *Glyceria fluitans*. If the surrounding water is more than 20 cm deep, many pairs add a ramp to the basic structure in order to protect the walls from damage during access. Egg nests are occasionally seen up to 8 m above ground level in dense bushes, possibly in abandoned nests of magpie or woodpigeon (Sharrock 1976).

Table 6.8 Food items of moorhen (Cramp *et al.* 1980)

Entire	Duckweed (<i>Lemna</i>)	Rush (<i>Juncus</i>)	Reed (<i>Phragmites</i>)
Leaves/stems	Pondweed (<i>Potamogeton</i>) Brooklime (<i>Veronica</i>)	Grasses (<i>Gramineae</i>)	
Seeds	Reedmace (<i>Typha</i>) Sedge (<i>Carex</i>) Waterlilies (<i>Nymphaea / Nuphar</i>)	Bur-reed (<i>Sparganium</i>) Dock (<i>Rumex</i>) Buttercup (<i>Ranunculus</i>)	Pondweed (<i>Potamogeton</i>) Bistort (<i>Polygonum</i>) Elm (<i>Ulmus</i>)
Berries	Yew (<i>Taxus</i>) Rose (<i>Rosa</i>) Sea Buckthorn (<i>Hippophae</i>)	Blackberry (<i>Rubus</i>) Hawthorn (<i>Crataegus</i>) Ivy (<i>Hedera</i>)	Rowan (<i>Sorbus</i>) Buckthorn (<i>Rhamnus</i>) Elder (<i>Sambucus</i>)
Fruits	Waterlily (<i>Nymphaea</i>)	Plum, pear & crab-apple (<i>Pyrus</i>)	
Invertebrates	Clams and snails (Mollusca) Bugs (Hemiptera) Moths and butterflies (Lepidoptera)	Spiders (Araneae) Caddisflies (Trichoptera) Flies (Diptera)	Harvestmen (Opiliones) Beetles (Coleoptera)
Vertebrates	Amphibia (tadpoles)		

6.5.4 Diet

The moorhen is omnivorous, taking food from the water and on land (Cramp *et al.* 1980: see Table 6.8). Aquatic food items are generally taken by dipping the head below the surface rather than diving, whilst terrestrial items are snatched at with the beak.

6.6 Water rail (*Rallus aquaticus*)

6.6.1 Habitat summary

- Distribution See map (Figure 6.19): lentic and lotic.
- Margin form Flat muddy ground.
- Marginal vegetation Emergent: *Phragmites* and *Typha* beds, osier beds, willow, cotton grass, bog myrtle and *Sphagnum*.
- Forb layer Dense, tall.
- Diet Omnivorous: plants most important in autumn/winter.

6.6.2 Introduction

The water rail (*Rallus aquaticus*) is a secretive bird which inhabits dense riparian vegetation such as *Phragmites* and *Typha* beds along rivers, lakes and overgrown canals. It may also be found in osier beds, carrs, sand/gravel pits, swamps, fens and acid bogs (with cotton grass, bog myrtle, willow and *Sphagnum*). The basic habitat requirement is freshwater associated with flat, muddy ground and dense, reasonably tall vegetation cover. Quite small habitats with such conditions may be sufficient.

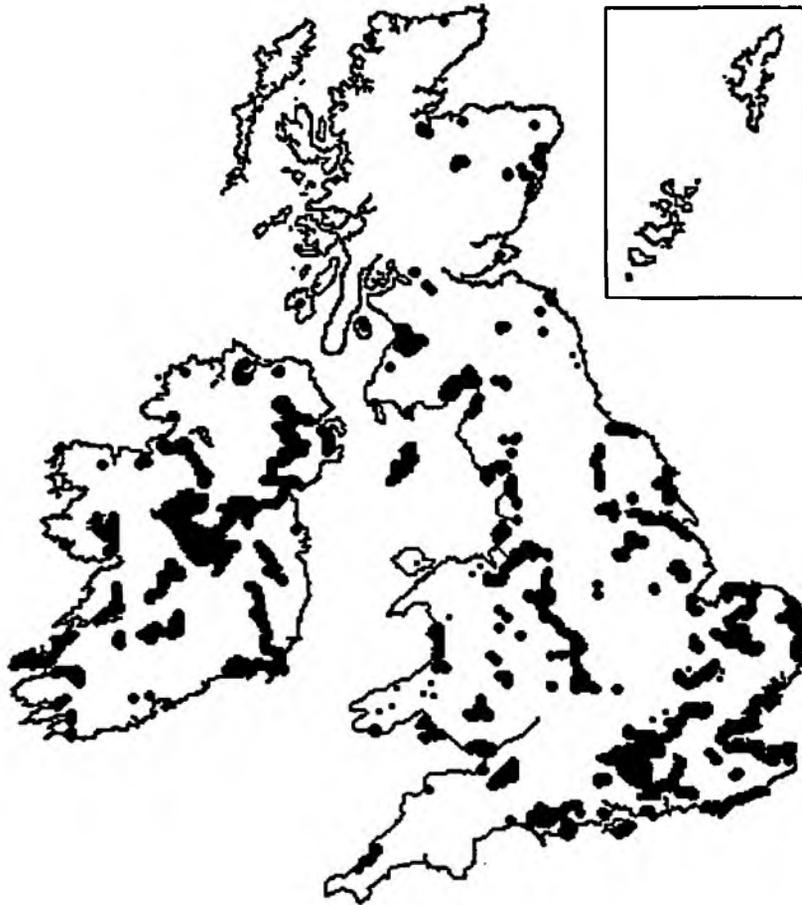


Figure 6.19 Broad distribution of the water rail in the British Isles (Sharrock 1976)

The water rail weaves rapidly amongst reed beds, crossing soft muds and floating vegetation with the aid of its long-toed feet. When disturbed, the water rail freezes and effectively blends in with surrounding reeds. The bird is difficult to detect, except after sunset by its 'sharming' – a call sequence which consists of a 'squeal-grunt-scream'.

6.6.3 Breeding

The nest is built by both sexes and is similar in construction to those of the moorhen, but smaller; found close to water on the ground amongst dense vegetative cover. In contrast to the moorhen, obvious trampled pathways are not found around the nest. The water rail begins egg-laying in the last week of March, with the last eggs hatching by early August (Cramp *et al.* 1980). Incubation, mostly by the female, takes 19-22 days. The care of the hatchlings is initially by bill-to-bill feeding; fledging occurs after 20-30 days, and the young become independent after about 55-60 days.

6.6.4 Diet

The water rail is omnivorous and may even take other birds if no other food is available (Sharrock 1976, Cramp *et al.* 1980, Wood 1986). Water rails forage in shallow water, feeding on and below the surface and in emergent vegetation. Insects and their larvae are important

food items throughout the year, mostly supplemented by plant foods in the autumn and winter (Cramp *et al.* 1980: see Table 6.9).

Table 6.9 Food items of water rail (Cramp *et al.* 1980)

Invertebrates	Caddisflies (Trichoptera)	Earwigs (Dermaptera)	Water bugs (Hemiptera)
	Dragonflies (Odonata)	Flies (Diptera)	Moths (Lepidoptera)
	Beetles (Coleoptera) e.g. Carabidae, Hydrophilidae, Dytiscidae, Staphylinidae, Curculionidae		
	Snails (Mollusca) e.g. <i>Bulinus</i> , <i>Zonitoides</i> , <i>Helix</i> , <i>Lymnaea</i> , <i>Planorbis</i> , <i>Pisidium</i> , <i>Bithynia</i>		
	Worms (Oligochaeta)	Leeches (Hirudinea)	Strimps (Gammaridae)
Vertebrates	Crayfish (Astacidae)	Spiders (Araneae)	
	Frogs, toads, newts (Amphibia)	Fish e.g. eel (<i>Anguilla</i>), bullhead (<i>Cottus</i>)	
	Birds and eggs	Small mammals	
Plants	Shoots and roots e.g. <i>Rorippa nasturtium-aquaticum</i>		Seeds, berries, fruits

6.6.5 Range

Water rails are not found in the mountainous country of the Pennines; Scottish Borders or Highlands; or higher ground of North Wales. The water rail is generally commoner in Ireland than in Britain.

6.7 Dipper (*Cinclus cinclus*)

6.7.1 Habitat summary

- Distribution See map (Figure 6.20)
- Altitude Breeds 0-600 m; maximum breeding densities at 90 -250 m
- Geology Calcareous: 60 - 150 mg CaCO₃ l⁻¹
- Gradient High, upstream: (0.6-)14-30(-38) m km⁻¹
- pH Circumneutral or alkaline.
- Flow regime Riffle-pool sequence.
- Vegetation Aquatic plants sparse or absent.
- Territory size Variable, dependent on habitat quality, 0.3-2.5 km
- Nest sites Rockfaces, crevices, overhangs, mudbanks, tree roots.

6.7.2 Introduction

Dippers are wren-like in shape; but typically of 180-210 mm body length and 250-300 mm wing span. The family (Cinclidae) consists of five species of which the American dipper (*Cinclus mexicanus*), the brown dipper (*Cinclus pallasi*) of eastern Asia and the European white-breasted dipper (*Cinclus cinclus*) are the most common. There are several subspecies of the European bird, two of which are resident in the British Isles. *Cinclus cinclus hibernicus* is to be found in Ireland, the Outer Hebrides and western Scotland; whilst *Cinclus cinclus gularis* occurs in the Orkneys, east and central Scotland, England and Wales. It is the latter with which this review is primarily concerned.

British dippers are typically of dark brown/black mottled plumage, with a dull, chestnut-brown head and ventral surface separated by a white bib. Juveniles have a dull grey mottled plumage with an off-white breast. Adult males are generally heavier than females although some overlap may occur: 60-80 g and 50-65 g respectively.



Figure 6.20 Broad distribution of the dipper in the British Isles (Sharrock 1976)

6.7.3 Range

The last nationwide survey of the British Isles' dipper population, performed by the BTO and the Irish Wildbird Conservancy, revealed a clear north-western range (see Figure 6.20). Dippers are absent from south-east England, East Anglia and the east Midlands; their range extends over the remainder of mainland Britain except for the Cheshire Basin and the Somerset Levels. Dippers also bred on the Isle of Man prior to 1950 (Parslow 1973: cited by Cramp *et al.* 1988). In the 1970s, the bird was resident across 53% of the British Isles by 10-km squares. The range during the early 1970s was found to be spreading south-eastwards into the Midlands, with an estimated national population of approximately 30 000 (Sharrock 1976).

6.7.4 Migration

Juveniles usually travel 3-4(-30) km from the natal site to establish their own breeding territories (Tyler *et al.* 1990). Females were found to account for 62% of movements over

5 km, probably due to displacement from territories by the heavier males. The majority of post-natal movements occur along water courses but some birds (mainly female) move between catchments to establish new territories (Galbraith and Tyler 1982, Mawby 1961, Tyler *et al.* 1990). Re-population of vacant but potentially suitable streams can therefore occur, following pollution events or winter mortality. Juveniles from warmer limestone streams re-populated streams on gritstone geology in Derbyshire following the severe winters of 1962 and 1963 (Shooter 1970).

Other migratory trends have been observed. Dippers will only ever breed, and most often overwinter, on steep fast-flowing streams. During the most severe winters, birds may overwinter on lowland rivers or even coastal estuaries. During the most severe continental winters, the central European Dipper (*Cinclus cinclus aquaticus*) may occasionally migrate to the south-east English coast to feed on small coastal streams or estuaries (Tyler and Ormerod 1988).

Dippers seek roosting sites close to their feeding territories during winter (Ormerod and Tyler 1990). Sheltered sites are chosen: often under bridges with suitable ledges, in drainpipes, natural rock ledges and crevices, or abandoned summer nests. Birds rarely travel more than 1 km to their roosts. They usually roost individually or in pairs, although juveniles will congregate in groups of up to eight or nine.

6.7.5 Breeding

During the breeding season, pairs establish a defended territory, in which they usually remain for the entire breeding season (Tyler *et al.* 1990). Dippers build football-sized nests of moss, grass and leaves. Terrestrial mosses and grasses are readily found along almost all streams (Tyler and Ormerod 1988) but they will travel some distance to collect leaves if trees are absent from the territory (Mawby 1961). Nests are usually located about 1 m vertically above the mean water level and rarely more than 1.5 m horizontally from the water margin. Preferred nesting sites are those offering sheltered protection from both terrestrial and airborne predators. Typical natural nesting locations include rock faces, cracks, crevices and overhangs, mudbanks, beneath tree roots, and behind waterfalls (Mawby 1961, Hewson 1967).

Many dippers nest using artificial features such as drainpipes, bridges, walls, and the bankside edges of weirs, culverts and sluices (Mawby 1961, Hewson 1967). Cramp *et al.* (1988) suggested that natural or artificial nesting sites are used according to their relative abundance. Mawby (1961) observed 19 nests from a total of 44 to be built on artificial structures, whereas Robson (1956) observed only 7 artificial sites from 53. Hewson (1967) reported that all nests within his study area on the River Towiemore were located on metal girders beneath a railway bridge – no riverside rockfaces were available at that site. Nesting success rate of the central European dipper (*Cinclus cinclus aquaticus*) was found to be 22-84% on natural sites but 94% in nesting boxes (Jost 1970).

6.7.6 Diet

The diet of the dipper consists mainly of benthic macroinvertebrates, supplemented by small fish. The first quantitative study of dipper diet was performed during the breeding season (April to May) in Perthshire (Da Prato and Langslow 1976). The diet was dominated about equally by adults and larvae of Trichoptera, Ephemeroptera and Plecoptera, with a small proportion of adult mosquitoes. Trichoptera and Ephemeroptera have subsequently been shown to be of greater importance than Plecoptera to both breeding and winter diets (Ormerod *et al.* 1985b). Adult insects are often taken whilst wing-drying after emergence from the river.

The importance of fish to the breeding diet was estimated by Ormerod and Boilstone (1985) using faecal pellet analysis. Young brown trout, minnows, bullheads and stone loach can contribute 14% of the diet by weight; providing an important source of calcium for egg formation.

The winter diet of dippers is more varied than that of the breeding season. This reflects opportunist exploitation of available prey, compared with the highly selective breeding diet (Ormerod and Tyler 1986). The relative importance of fish increases in the winter diet; and Diptera, Mollusca and Crustacea are also eaten. Table 6.10 shows recorded winter diet and Figure 6.21 compares the winter and breeding dietary composition on Welsh streams.

Table 6.10 The winter diet of dippers on the River Wye (Ormerod and Tyler 1986)

Item	% numbers	% weight	Item	% numbers	% weight
Mollusca	5.2	6.1	Trichoptera	23.3	19.4
Crustacea	5.4	3.2	Coleoptera	0.1	0.1
Ephemeroptera	18.0	3.2	Diptera	33.4	3.1
Plecoptera	11.3	1.3	Fish	1.7	63.7
Hemiptera	0.3	0.1			

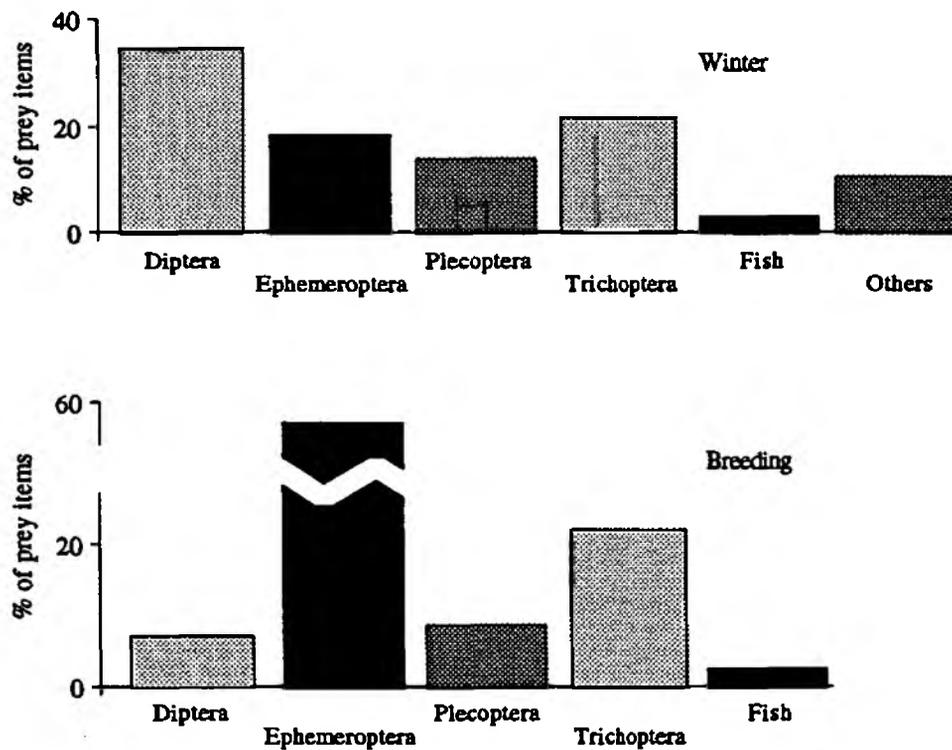


Figure 6.21 Breeding and winter diets of the dipper (Tyler and Ormerod 1988)

6.7.7 Water quality

The most influential form of pollution on dipper populations appears to be stream acidification, studied by Ormerod and collaborators (Ormerod *et al.* 1985b, 1985a, Ormerod

and Tyler 1986, 1987, 1991, Ormerod 1988, Tyler and Ormerod 1988) and Vickery (1991). Figure 6.22 shows the effect of stream acidity on populations along the upper tributaries of the River Wye (Ormerod *et al.* 1985b) and upland streams in south-west Scotland (Vickery 1991). A long-term drop in dipper numbers has occurred on the Wye, with the population density falling between 1963 and 1984 in parallel with decreasing stream pH. Such trends appear to apply nationally (Tyler and Ormerod 1988).

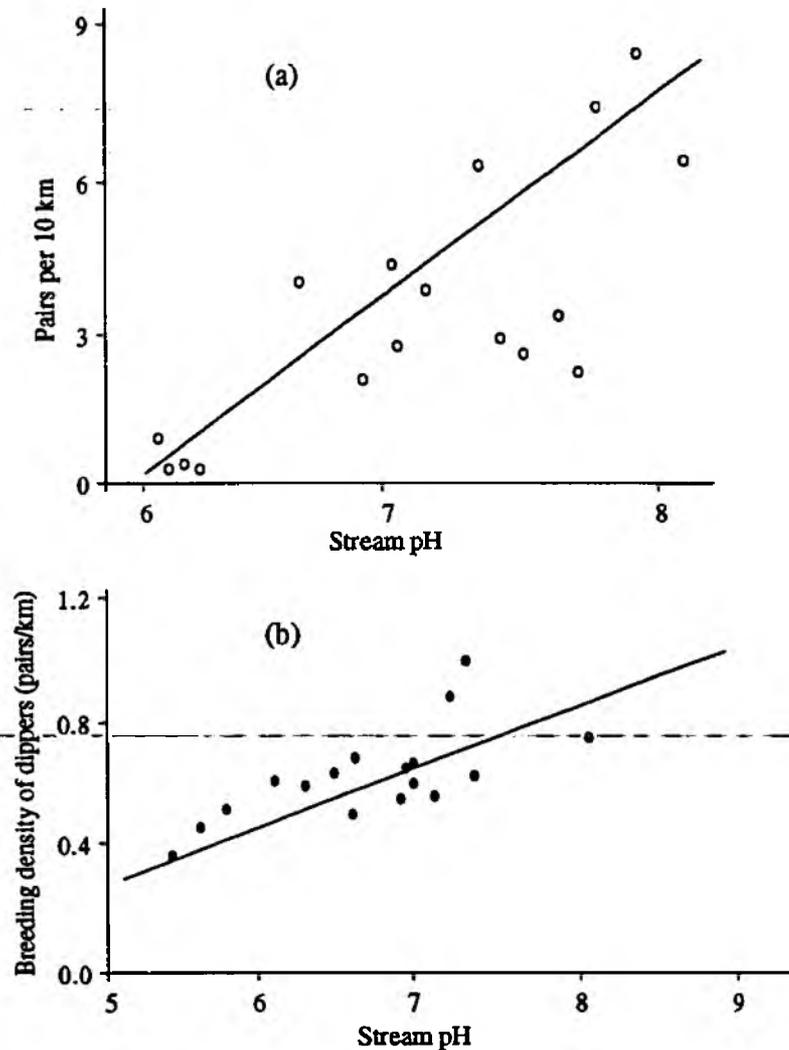


Figure 6.22 Stream pH and breeding dippers on (a) the upper tributaries of the River Wye (Ormerod *et al.* 1985b); and (b) on upland streams in SW Scotland (Vickery 1991)

The link between stream acidification and dipper population decline is most probably dietary: a decrease in macroinvertebrate abundance. Krueger and Waters (1983) found macroinvertebrate populations, especially of Ephemeroptera and Trichoptera, decreasing with acidity in Minnesota. Buffering capacity is reduced by acidity, with consequent mobilisation of metals and lowered rates of organic detrital decomposition and flocculation of dissolved organic matter. Stream acidification promotes levels of aluminium and manganese, and decreases the availability of calcium in streams (Harriman and Morrison 1982). The pH-related changes in

macroinvertebrate biomass and composition in south-west Scotland are shown in Figure 6.23 (Vickery 1991). Populations of Ephemeroptera and Trichoptera have been found to decrease with stream acidity on the River Wye (Ormerod *et al.* 1985b), although Plecoptera seem to be less vulnerable.

Harriman and Morrison (1982) showed upland conifer plantations to be a major cause of stream acidification in Britain, in addition to the contribution of acid precipitation in upland areas. In Sutherland and Caithness, failure of the dipper appears to be related to stream acidification, coinciding in turn with coniferous afforestation of peat bogs (Ratcliffe 1990). Aluminium toxicity affects macroinvertebrates which form the majority of the dipper's diet. The impact of decreased calcium availability on fish and Mollusca also reduces dipper breeding success, due to smaller clutch size and potential clutch failure from egg shell thinning (Ormerod *et al.* 1988).

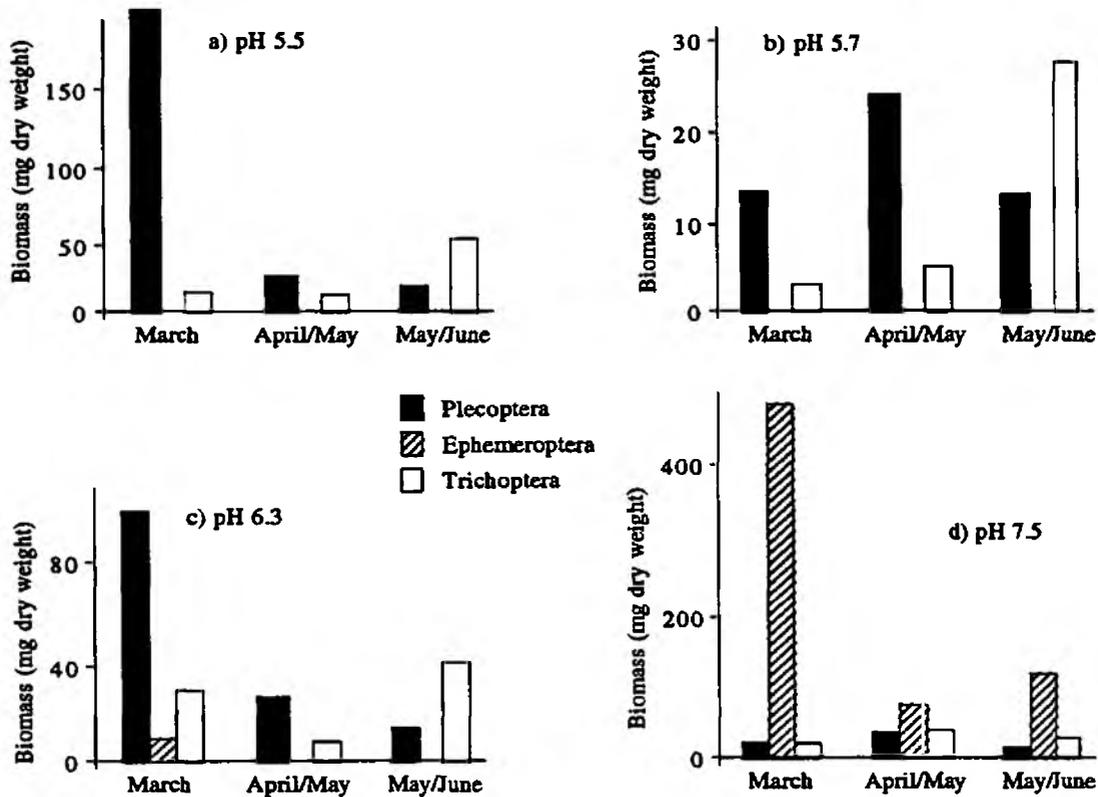


Figure 6.23 Biomass of three macroinvertebrate taxa and stream pH (Vickery 1991)

Dipper abundance has been shown to be directly proportional to the availability of pH-sensitive Trichoptera and Ephemeroptera (Ormerod *et al.* 1985b, see Figure 6.24). Plecoptera appear to be less vulnerable to a fall in stream pH and they consequently account for a high proportion of the diet on acid streams (Ormerod and Tyler 1991). Adult dippers may therefore successfully winter in acidified catchments (Ormerod and Tyler 1986); but breeding success is unlikely without sufficient fish, Trichoptera and Ephemeroptera to supply the required high energy and calcium demands of egg gestation and rearing nestlings (Ormerod *et al.* 1985b). Territory lengths increase with acidification, as breeding pairs need to cover longer reaches of stream corridor to collect sufficient food. Vickery (1991) found a strong correlation in which territories were twice as long at pH 5.5 than at pH 7.5.

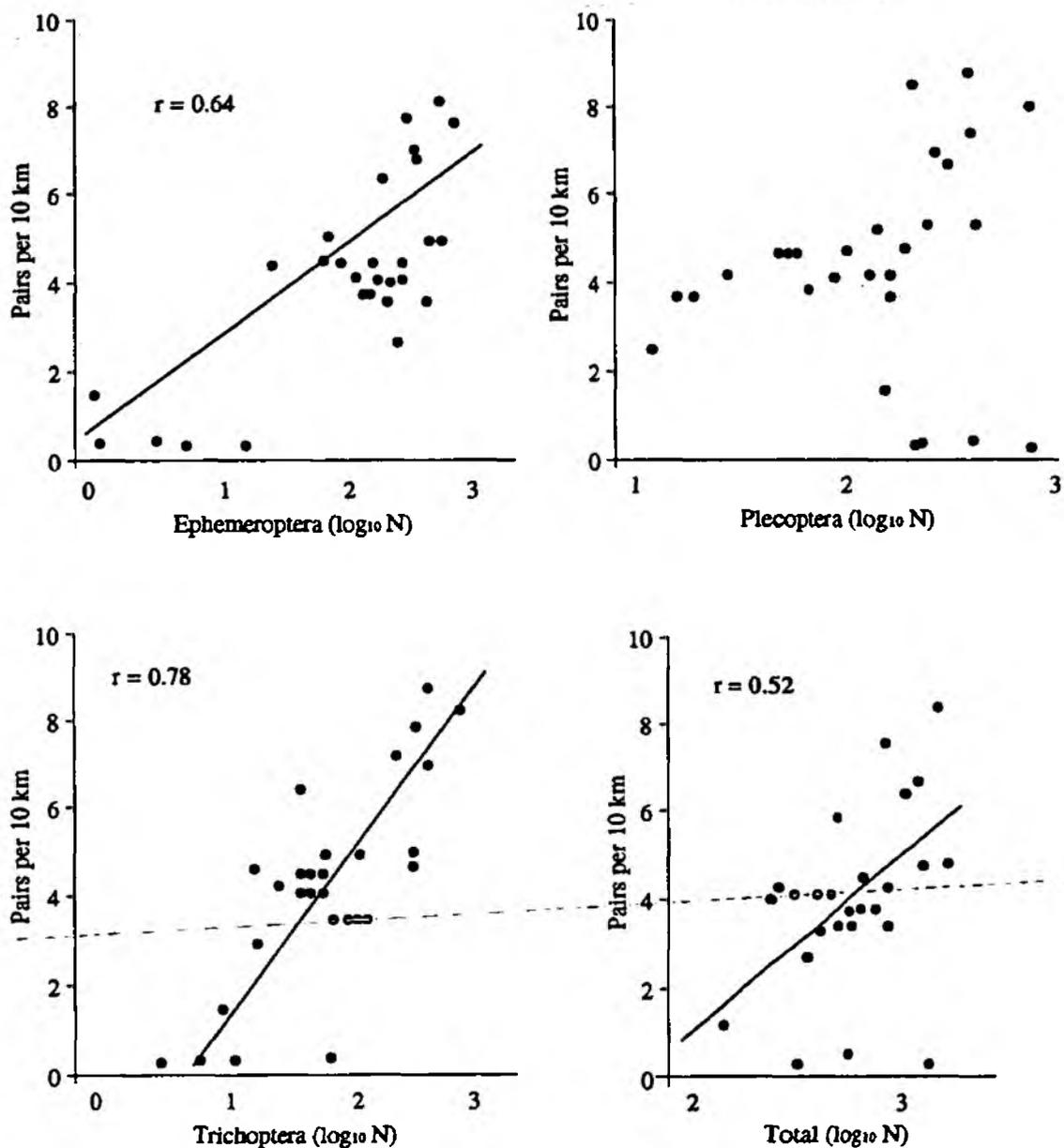


Figure 6.24 Abundance of breeding dippers and invertebrates (Ormerod *et al.* 1985b)

Stream acidification is not the only pollution problem affecting dippers. Coal waste, silage runoff and farm slurry, agricultural pesticides and poorly treated domestic sewage or industrial effluent can all reduce food availability and damage otherwise suitable habitats (Tyler and Ormerod 1988). Streams passing through or alongside areas of intensive agriculture, industry, mining or urbanisation are most likely to experience a deterioration in habitat value.

6.7.8 Feeding and channel morphology

Dippers are unique amongst passerines in that they may feed by both wading and diving/swimming. Diving consumes more energy than wading (Bryant and Tatner 1988) and

thus shallow waters (feeding by wading) are preferred almost exclusively to waters which require diving (Shooter 1970, Marchant and Hyde 1980). Diving for food usually takes place only when streams become swollen and flooded during the winter months (Tyler and Ormerod 1988).

Dippers typically feed by wading across the river bed and overturning small stones to reveal macroinvertebrates and small fish. Thus shallow, stony riffles (often with little or no vegetation) are strongly preferred feeding sites (Cramp *et al.* 1988). The dipper's range and population density appear to be strongly related to the availability of such riffles (Shooter 1970). The bird is well-adapted to fast flowing waters and thus benefits from a specialized niche (Ormerod and Tyler 1987).

The primary control on the availability of suitable shallow riffles is stream gradient. High-gradient streams with well-developed riffle sequences generally occur at higher altitudes. The dipper therefore has a strong preference for upland areas; is commonly associated with mountain streams; and is absent from most of lowland Britain. At the highest altitudes, population density decreases due to the shortened breeding season and severe winter frosts (Marchant and Hyde 1980). Shooter (1970) observed maximum breeding densities at about 90-250 m above sea level in Derbyshire. Gradient, rather than altitude, is the controlling factor: Tyler and Ormerod (1988) found breeding dippers from sea level to 600 m in mountainous coastal and inland areas of Scotland and Wales.

Gradient as a control on suitable feeding sites has also been the subject of quantitative studies. A national mean of 14 m km^{-1} was estimated for dipper territory stream gradient by Marchant and Hyde (1980). Ormerod *et al.* (1985b) reported typical slopes of $15\text{-}30 \text{ m km}^{-1}$ from the Rivers Wye and Grwyne Fawr in south Wales. A range of $0.67\text{-}38.1 \text{ m km}^{-1}$ was observed by Round and Moss (1984) on the Rivers Wye and Severn. Below gradients of 0.67 m km^{-1} rivers are generally too deep to provide suitable feeding sites, whilst gradients above 38.1 m km^{-1} are associated (through altitude) with winter conditions too severe for dippers.

The mean area of shallow gravel riffles required by a pair of breeding dippers has been estimated at approximately 4000 m^2 (Shooter 1970). Shooter found typical territory lengths of 1.6 km, where one third was comprised of suitable riffle feeding sites. A national range of 0.3-2.5 km territory length has been estimated (Ormerod and Tyler 1987, Tyler and Ormerod 1988). Ormerod *et al.* (1985a) found about 100 pairs over 220 km in the River Wye catchment with typical densities of 2.9-8.5 pairs per 10 km; greatest on streams of steepest gradient and circumneutral to alkaline pH. Another study in upland Wales found densities of 1.15-2.67 pairs per 10 km (Round and Moss 1984).

6.7.9 Geology

Robson (1956) found 2.1 dipper pairs per 10 km on limestone geology and 6.2 pairs per 10 km on sandstone in Cumbria. Similar densities were found on gritstone (5.4 pairs per 10 km) and limestone (5.8 pairs per 10 km) by Shooter (1970) in Derbyshire. Differences have been attributed to higher mean temperatures of groundwater from different rock types, influencing the likelihood of surface freezing in winter. A more important factor could be the effects of water hardness. Dippers are known to prefer streams of hardness 60-150 $\text{mg CaCO}_3 \text{ l}^{-1}$ with circumneutral or slightly basic pH (Ormerod *et al.* 1985b). Such streams are typically found over calcareous geology and have greater buffering capacity than those flowing in acidic geology.

Porous limestone is typified by relatively few surface streams whereas gritstone geology bears a high drainage density, with a larger number of surface tributaries and associated

suitable habitats. Thus population densities by area rather than stream length are higher on gritstone (Shooter 1970). Populations on gritstone are able to recover well from drought or severe winters, due to the abundance of suitable habitats.

6.7.10 Biotic interactions

Despite territoriality within the species, dippers tolerate many other species in close proximity, even species with similar dietary and nesting needs. Grey wagtails and common sandpipers often occupy the same areas as the dipper, but wrens are often displaced (Mawby 1961, Tyler and Ormerod 1988). The kingfisher may displace dippers from a territory despite its smaller size.

The mean annual mortality rate of juveniles (first-year birds) has been estimated at around 64%, whereas adult mortality rates are 40-47% (Galbraith and Tyler 1982). The dipper has a large number of natural predators (listed by Tyler and Ormerod 1988) although human interference of nests is believed to account for a high degree of breeding failure (see Section 6.7.11). The ranges of the sparrowhawk, kestrel and crow all coincide with that of the dipper in the British Isles (Sharrock 1976) – as partially do the ranges of the tawny owl, magpie, peregrine and merlin. A number of mammals prey upon the dipper, mostly on its nests. The rat is more or less ubiquitous but population densities are highest adjacent to built-up areas, farms and sewer/drain outfalls. Domestic cats (Tyler and Ormerod 1988), mink, weasel, stoat and the domestic cat are found over much of the dipper's range; the polecat co-occurs in Wales only.

From a limited number of observations made near Sedbergh, Mawby (1961) concluded that thick wooded shelter from predators along stream corridors was not an important habitat requirement. Dippers are most vulnerable to predation during the moult (late June to early July) when loss of wing and tail feathers reduces their flight performance. Then the bird lies amongst tree roots or avoids predators effectively by diving into streams and swimming away from danger, so there is not a significant change in the mortality rate for this period (Tyler and Ormerod 1988).

6.7.11 Human impacts

The greatest human impact on dipper habitat is water pollution, most notably stream acidification in upland areas as described in section 6.7.7.

Man has acted as a direct 'predator' of the bird within its habitat. For many years dippers were believed to take a large number of small fish, thus making a significant impact on stream trout stocks. Consequently dippers were trapped and shot to preserve the quality of fishing. Persecution is now, however, a rare and localised problem (Tyler and Ormerod 1988). Although fish make an important contribution to the bird's diet by mass, the absolute number of fish taken is very low, thus making an insignificant impact on fish stocks (Ormerod and Boilstone 1985); and this is accepted by most. A significant cause of breeding failure may be the disturbance of nests and the breaking or removal of eggs, where streams are close to habitation and have sufficient access (Shooter 1970, Tyler and Ormerod 1988).

River engineering can degrade dipper habitat. Channelisation or bank maintenance may damage nesting sites, whilst work in the channel often involves removal of riffle material or wholesale degradation of the long profile. The flooding of deep upland valleys for reservoir construction in Derbyshire has resulted in the loss of many breeding territories (Shooter 1970).

Not all human impacts on habitat are negative. Dippers strongly prefer shallow riffle feeding sites usually found on steep gradient upland streams. However, suitable feeding sites

may be created incidentally by the building of weirs or culverts, causing an increase in flow velocity and an associated shallow gravel bed (Sharrock 1976). Artificial structures such as revetments may also provide nest sites. Population densities and breeding success have been found to be higher along streams close to farmsteads in agricultural areas, as dippers may supplement their aquatic diet with the insects found in abundance around farm buildings (Robson 1956, Mawby 1961, Cramp *et al.* 1988).

6.8 Plovers (*Charadrius* spp.)

6.8.1 Habitat summary

Ringed plover (*Charadrius hiaticula*)

- Distribution See map (Figure 6.25): mainly coastal.



Figure 6.25 Broad distribution of ringed plover in the British Isles (Sharrock 1976)

- Marginal zone Sandy shingle/shell beaches and gravel pits. Avoids steep rocky areas or mudflats.

- Terrestrial vegetation Dry 'machair' (Western Isles)
- Isolation Island sites: offshore, nature reserves.
- Territory size 0.3-10 ha or more.
- Human disturbance Sensitive.

Little Ringed Plover (*Charadrius dubius*)

- Distribution See map (Figure 6.26).
- Marginal zone Shingle beds on or near coast, gravel pits, sewage farms, soil heaps.

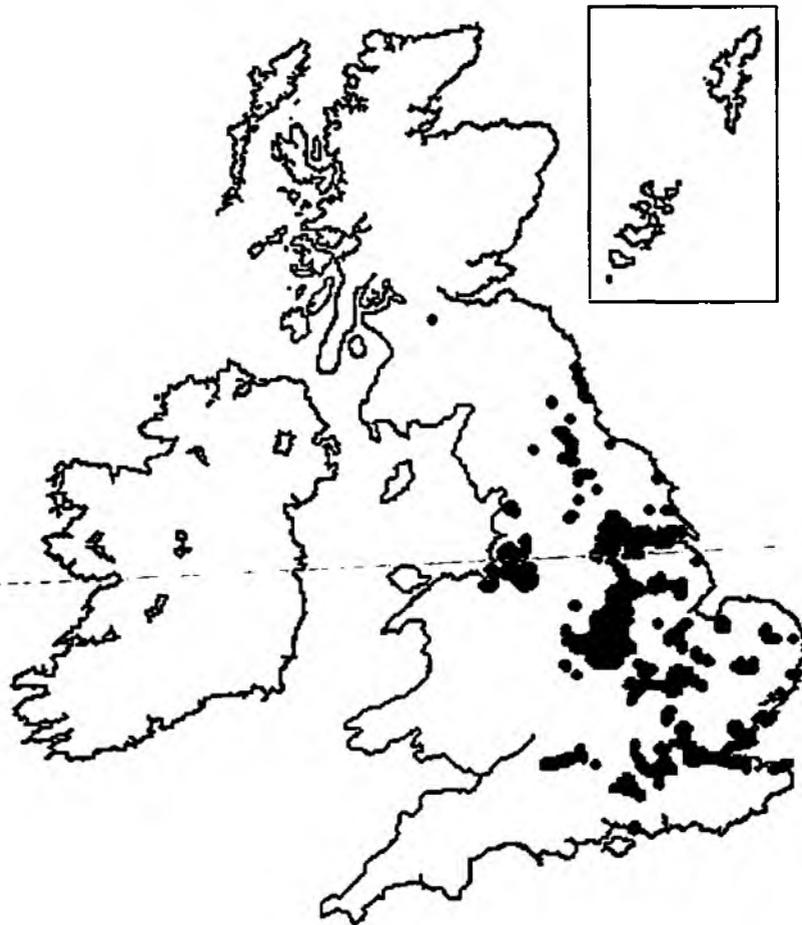


Figure 6.26 Broad distribution of little ringed plover in British Isles (Sharrock 1976)

6.8.2 Introduction

Britain and Europe host a number of plover species, either as residents or common migrants, and each species has a distinct range of habitats (Table 6.11). The ringed plover and the little ringed plover are reviewed in this report because of their recent increase at inland sites.

Table 6.11 Habitats of British plover species (Vaughan 1980)

Species	Colloquial name	General habitat
<i>Vanellus vanellus</i>	Lapwing	Fields, moorland, flat sea shores
<i>Pluvialis squatarola</i>	Grey plover	Flat sea shores
<i>Pluvialis apricaria</i>	Golden plover	Fields in winter, moorland in summer
<i>Charadrius morinellus</i>	Dotterel	Fields in spring and autumn, mountain tops in winter
<i>Charadrius hiaticula</i>	Ringed plover	Flat sea shores
<i>Charadrius alexandrinus</i>	Kentish plover	Flat sea shores - rare in Britain
<i>Charadrius dubius</i>	Little ringed plover	Gravel pits, rivers

In the British Isles, the ringed plover breeds primarily on the coast; although during the last twenty years there has been an increasing tendency to nest inland, particularly in northern England and Scotland. Over 90% of the English and Welsh plover populations are coastal, with 70% being found on sandy shingle or shell beaches. Since the pressures on this habitat have become considerable, many ringed plovers (especially in south England) have nested in power stations and oil refineries and on farmland adjacent to sea walls. A wide variety of sites are used inland, such as shingle banks of rivers and lakes, reservoirs and gravel pits.

Little ringed plovers were unknown in Britain before 1938, when a pair nested in Hertfordshire. By 1972, 400 pairs were recorded in Britain. The species is protected under Schedule 1 of the Protection of Birds Act. In continental Europe, little ringed plovers usually nest on shingle beds in rivers, some on or close to the coast. In Britain the majority of breeding pairs have been observed at gravel pits, sewage farms, reservoirs, industrial tips and waste ground; though some rivers, especially in Wales, have fair numbers. The spread of the little ringed plover in the UK has coincided with increased numbers of gravel pits (Sharrock 1976).

6.8.3 Breeding

Studies on the factors limiting breeding distributions and determining timing of breeding have concentrated on food supply.

Britain and Greenland form the southern and northern limits of the breeding range of ringed plovers. In northern parts of their breeding range, they nest both inland and near the coast on barren land such as stony ground and river gravels. At lower latitudes, however, plover habitats are restricted to coastal regions. A study in Greenland (Pienkowski 1980) found ringed plover nesting sites mainly on river-bed shingle and sparse tundra heath. Plovers breeding in England have a longer time in which to establish their territories in comparison to their conspecifics in Greenland, with some birds remaining in England throughout the year (Pienkowski 1980). In England, ringed plovers nest on shorelines close to inter-tidal areas where they feed. They avoid steep rocky areas, and sites where mud flats and *Spartina* marshes reach the high water mark.

Ringed plovers generally return to the same territory in consecutive years. Pienkowski (1980) recorded variable territory sizes on Lindisfarne: territories as small as 0.3 ha were well-defined on the north shore, whilst elsewhere more diffuse territories of over 10 ha were common. In England, territorial behaviour is maintained throughout the breeding season, possibly because of small, closely-spaced territories and repeated nesting attempts. The extent of feeding within the territory varied on Lindisfarne; family parties obtained most of their food from within their territory in the late season.

Pienkowski (1984) found that most birds travel to a breeding area and attempt to breed when one year old. The laying date of the first egg varied over a range of several months; the

mean clutch size was 3.84 eggs and clutches were incubated for a mean of 23.5 days. Ringed plovers exploit the high summer availability of food (notably Diptera) for best growth of their young (Holmes 1986). Other factors, such as the high risk of nest predation early in the season, also influence the time of breeding. The probability of a clutch surviving to hatching when laid before mid-May at Lindisfarne was only 3% (Pienkowski 1980). The seasonal variation in the incidence of predation may be related to increases in alternative foods for the predators.

Variations in nest survival on a wide geographical scale may be related to predation intensity and to the quality of available habitat in which to nest. Generally, the variety and population densities of potential predators increases at lower latitudes, whilst the extent of bare ground decreases (being restricted mainly to shorelines). The combination of increased predation and decreased bare ground limits the southern extent of the breeding distribution.

Survival from hatching to fledging is about 40-60% in different areas and years. Nest losses may be caused by spring flooding; covering by blown sand; or a fairly wide range of predators. At least 60% of birds survive from fledging to one year and the minimum survival between one and two years age is similar. The annual survivorship of older birds is higher - at least 80% for breeding adults. There are indications that the ringed plover in Britain is only self-supporting at sites where it receives some form of natural or artificial protection, such as offshore sites not colonised by ground predators, or nature reserves (Pienkowski 1984). Annual mortality of nesting adults on Lindisfarne was 20 %; thus breeding pairs need to produce an average of 0.4 surviving young per year, or be supplemented by net immigration from more successful locations.

6.8.4 Diet

Most waders are opportunistic invertebrate feeders (Smith 1975), taking the most abundant invertebrate species present (Pienkowski 1982). Plovers forage visually, waiting for prey to emerge or move; the birds run rapidly to catch and swallow the prey before resuming a waiting position; running to new waiting positions if no prey are detected. Plovers have fairly short bills and do not normally probe into the substratum (Pienkowski 1979). In a study conducted on the diet of ringed plover on Lindisfarne, polychaetes (*Arenicola*, *Notomastus*, *Scoloplos* and *Phyllodoce* spp.) provided the main food in terms of both numbers and energy content during the day (Pienkowski *et al.* 1980). Other food included bivalves, small amphipods and isopods which were taken mainly at high tide (Pienkowski 1982).

6.8.5 Abundance

The British population of little ringed plovers increased by 30% between 1973 and 1989, reaching at least 608 pairs; their range has extended westwards; and there has also been an expansion within the northern part of the existing range (Parrinder 1989). Numbers have changed very little in the south of England over the 16 year period. It is possible that the all of the suitable habitat in the south is now fully occupied, although competitive interaction with ringed plovers may also be a limiting factor in places.

The long term future of the little ringed plover in Britain may be less favourable, as it depends largely on man-made habitats (free from vegetation) for breeding. There is a wide divergence between the populations of the north and south of the country. In the south, 81% of the population depend upon man-made habitats, in particular gravel pits. In the 1984 census, about 35% of gravel pits and other quarry areas were described as disused, old, worked out, landscaped or restored and if they are left unmanaged, vegetation will gradually eliminate them as potential nesting grounds. In the north, 45% of little ringed plover reside in industrial areas, where spoil heaps often provide nesting sites and subsidence pools cater for their feeding

requirements. During low rainfall, reservoirs form important habitats due to an increase in muddy edges suitable for feeding, and extensive areas for nesting. Of 370 sites recorded nationwide, only 11 (i.e. 3%) were located on river shingle - the original nesting habitat of the species prior to its range expansion in the 1930s.

Where land is being developed for leisure purposes, provision can be made for little ringed plover by the construction of shingle pits or islands, or by leaving rough areas of ground adjacent to shallow water. However, such sites need continued management in order to keep the ground relatively free from vegetation.

A similar census was conducted in 1984 for the population numbers of ringed plovers (Prater 1989). Population size was estimated at 8600 territory-holding pairs, with 66% of these birds residing in Scotland. In particular, the dry 'machair' of the Western Isles supported 2324 pairs of ringed plover (27 % of the national total). In Scotland, the distinction between inland and coastal habitats is often unclear - maritime heathland, farmland, moorland and machair merge into sandy and shingle beaches and narrow sand-dune systems. Detailed studies on North and South Uist, Benbecula and adjacent small islands have shown that 71% of their ringed plovers breed on dry machair, especially when it is cultivated, so this provides a habitat model for the species. The estimated population numbers for England (2389) and Wales (224) showed increases of 19.6% and 21% respectively between 1973/4 and 1984. In England, there was a clear tendency for ringed plovers to colonise 'island' sites (including those on nature reserves), moving away from industrial relicts to natural sites such as sand dune belts.

The pressures exerted upon ringed plovers by unrestricted public access has been examined at Lindisfarne, where the survival rate to hatching of nests was investigated in relation to the number of human visitors (Pienkowski and Pienkowski 1989). It was found that when there were more than 50 visitors per day only 1.4-2% of nests survived; whereas with less than 50 visitors per day, survival increased to 21-33%; and with only 5 visitors per day a 43-58% survival rate was achieved (Pienkowski and Pienkowski 1989). Ringed Plovers establish their territories from February to late March. This is before the period of intense human activity - a site may appear to be ideal as a nesting and feeding area, later to be disturbed or trampled.

6.9 Wagtails

6.9.1 Habitat summary

Grey wagtail (*Motacilla cinerea*)

- | | |
|--------------------------|--|
| • Distribution | See map (Figure 6.27): hard waters. |
| • Water depth | Shallow. |
| • Flow velocity | Fast: rapids, waterfalls, weirs, lake outlets. |
| • Foraging habitat | Shingle banks. |
| • Gradient | At least 2.5 m km ⁻¹ |
| • Nest sites | Bridges, holes in walls etc. (about 1 m above water level) |
| • Terrestrial vegetation | Broadleaved woodland. |
| • Breeding density | Modal length 1.6 km (range 0.5-6.4 km) |
| • Human disturbance | Sensitive. |

Yellow wagtail (*Motacilla flava*)

- Distribution See map (Figure 6.28)
- Geology Avoids dry, upland chalk.
- Terrestrial vegetation Grass tussocks.
- Shelter features Hollows, banks.

Pied wagtail (*Motacilla alba*)

- Distribution See map (Figure 6.29)
- Nest sites 0-1.5 m above ground level: in banks, cliffs, buildings and abandoned nests of other birds.
- Human disturbance Sensitive.

6.9.2 Grey wagtail (*Motacilla cinerea*)



Figure 6.27 Broad distribution of the grey wagtail in the British Isles (Sharrock 1976)

Grey wagtails are found primarily along shallow, fast flowing water (e.g. mountain streams) and are often seen in the same location as dippers. In addition, they are found along fast-flowing sections of lowland streams (e.g. mill races, weirs). Nesting is usually in holes close to the water.

They are common in the hilly areas of the north and west of Britain, and their numbers are increasing in eastern and southern England. Grey wagtails are absent from some areas in parts of East Anglia, the eastern Midlands and Lincolnshire.

Grey wagtails can be severely affected by bad winters, during which upland birds may migrate to lower areas and can be found around cress beds and sewage farms. If the lowland streams freeze, only those birds that reach the coast or migrate to France are able to survive; this susceptibility to weather conditions leads to frequent population fluctuations.

6.9.3 Yellow wagtail (*Motacilla flava*)

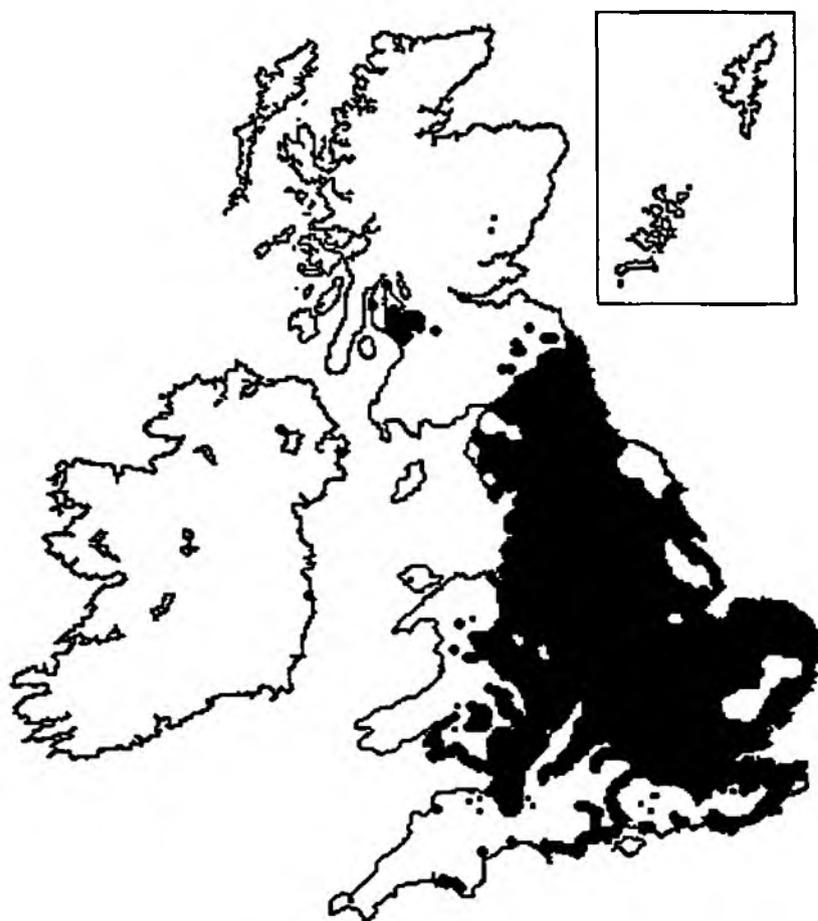


Figure 6.28 Broad distribution of the yellow wagtail in the British Isles (Sharrock 1976)

Yellow wagtails are only summer visitors to Britain, resident from April to the end of September, after which they leave to winter in west Africa. They are associated with water, breeding in damp river valleys and water meadows and freshwater margins in coastal areas; and are also found on grassland, arable land and dry heaths.

Yellow wagtails breed in most of England, but their numbers have fallen in Scotland and are probably absent from Ireland. They are not found on the 'dry' upland chalk areas of Britain but colonies are found nesting on heaths and moorlands. Yellow wagtails often feed amongst farm animals, snatching at insects stirred up by animals' hooves.

6.9.4 Pied wagtail (*Motacilla alba*)



Figure 6.29 Broad distribution of the pied wagtail in the British Isles (Sharrock 1976)

The pied wagtail is present in Britain all year round, although some British birds migrate to south-west Europe in winter. They breed more or less anywhere including cities, sea shores and streams; although they are the least likely of the three species to be found in the stream riparian zone. Pied wagtails are now more common in Ireland and Scotland than in eastern England where a change from mixed to mainly arable farming may have had an effect. The pied wagtail catches insects on the wing and roosts on a bank, cliff or man-made structure.

6.9.5 General habitat

An early work on yellow wagtails reported that the birds were often associated with river valleys, especially along the lower reaches (Smith 1950). Typical yellow wagtail habitat is

water meadow with cattle pastures and grazed semi-marshland - such areas provide nesting sites and food. Smith (1950) also noted that in lowland Britain, populations are to be found at sewage works - in Middlesex he believed population growth to have been associated almost entirely with sewage farm and reservoir construction. From BTO records for the species, Mason and Lyczynski (1980) found that 89% of Yellow wagtail nests were in rural areas and of these 52% were close to water, mostly in grasslands.

Over half of the BTO nest records for grey wagtails were in lowlands, but this reflects the distribution of observers more than that of the birds. Of 699 records, 695 nests were found in rural habitats and the four urban sites were on or beside sewage farms. The nests were close to rapidly flowing water such as waterfalls, weirs or outfalls of lakes or ponds; 97% were built very close to running water and the few that were away from running water were close to standing water (Tyler 1972).

Pied wagtails do not rely on the riparian zone as much as the other wagtail species. BTO nest records found 84.2% in rural habitats and 15.8% in suburban or urban habitats. Only 26.2% of pied wagtail nests were close to water (Mason and Lyczynski 1980).

6.9.6 Breeding

Site selection

Mason and Lyczynski (1980) showed that yellow wagtail nests were associated with wet sites and that 96% of the nests were on the ground. Of these, 79% were partially sheltered by tufts or tussocks of grass whilst others were in banks, hollows or under clods of earth.

Grey wagtails choose slightly different sites for nest building. They use holes in walls, bridges and banks. Artificial sites are most frequent; associated with bridges; and are often selected in preference to natural locations. Tyler (1970) found that 72% of nests not actually at a bridge were within 30 yards of one - although this may reflect recording bias. Away from bridges, a variety of sites may be colonised: holes, ledges or vegetation in the banks of streams or (particularly ivy) in walls; old huts and roofs of houses. Most nest sites were approximately 1m above the ground or water but Tyler (1972) did not report any nests found in trees.

Mason and Lyczynski (1980) found that more than half of pied wagtails nests were associated with buildings etc. - in contrast to yellow and grey wagtails. 20% of nests were in other artificial sites such as woodstacks, oil drums or rolls of netting. It was also found that pied wagtails used old nests of other bird species. Most of the sites were in holes, clefts, ledges of walls, bridges, locks or buildings, with a small proportion in steep banks, rock faces and sea cliffs. Half of the nests were recorded at sites above ground level but below 1.5 m high, and 24% between 1.5 and 3.0 m (the highest nest recorded was on a building 15.2 m up).

Breeding density

Grey wagtails, although commonest on harder water streams, occur and breed across a wide range of water chemistry. Vickery (1991) found breeding densities ranging from 0.14-0.56 pairs per km for streams in south-west Scotland. The density of breeding pairs was not significantly correlated with stream pH; other variables included physical structure, gradient, altitude and nature of bankside vegetation. Ormerod and Tyler (1987) found no correlation between breeding abundance and either altitude or river slope (which ranged between 3 and 60 m/km). However, they quoted a BTO study which showed that the mean

abundance of grey wagtails exceeded 6 pairs per 10 km provided that river slopes were not less than 2.5 m/km; and a study by Marchant and Hyde (1980) which found an increase in abundance of grey wagtails as altitude increased. Ormerod and Tyler suggested that the lack of any significant relationship in their study was due to the consistently high gradient of the streams (most exceeded 2.5 m/km) and that steep, suitable streams occur in the study area even near sea-level.

Tyler (1972) found that breeding density of grey wagtails varied from one pair per 6.4 km to one pair per 0.5 km (mode: one pair per 1.6 km) on New Forest streams. Lowest densities were apparent on base-deficient streams in the north and west of Britain. Tyler suggested that this was related to food availability. This view was supported by Ormerod and Tyler (1987) who concluded that birds were commonest on hard water streams with abundant aquatic invertebrates, though it has more recently been found that aquatic invertebrates may not be so important in the breeding density of the birds (Ormerod and Tyler 1991).

Timing

The three species seem to begin breeding at different times, with the pied wagtail and yellow wagtail breeding later than the grey wagtail. This may be correlated to some extent with their food preferences (Tyler 1972).

Temperature also influences the timing of breeding. Mean first-egg dates of the pied wagtail are later; and the proportion of clutches started in April is lower; when the mean April air temperatures are lower (Mason and Lyczynski 1980).

Nest failure

Causes of the failure of nests vary between species. The primary causes for yellow wagtails seem to be climatic effects and farming activities; both pied and grey wagtails are more vulnerable to predation (Mason and Lyczynski 1980). Humans seem to be a factor in the failure of pied and grey wagtail nests, probably because of their accessibility – often on or beside artificial structures.

6.9.7 Diet

Davies (1977) showed that pied and yellow wagtails feed almost entirely on Chironomidae along with large numbers of Drosophilidae. Changes in the diet over a period of time were related to changes in abundance of the preferred prey (Chironomidae); and as the numbers of these decreased, Drosophilidae were incorporated into the diet to maintain the feeding rate. Davies also observed pied and yellow wagtails foraging around dung for other Diptera and Coleoptera.

Grey wagtails are almost exclusively insectivorous, foraging opportunistically around streams (Ormerod and Tyler 1991). At moorland sites, prey captures from open ground are also important. Birds show a marked preference on streams for areas of shingle, ignoring trees and foraging less than expected directly from the stream. Only 25% of the diet of grey wagtails is formed by aquatic insects including Diptera, Trichoptera, Ephemeroptera and Plecoptera (Ormerod 1987). By foraging in a variety of habitats grey wagtails avoid reliance on aquatic sources, with prey of both terrestrial and semi-aquatic origin important in their diets. About 55% of the aquatic insect prey may be Diptera (Empididae, Syrphidae, Ephydriidae, Trichoceridae, Tipulidae and Chironomidae), with Trichoptera, Ephemeroptera and Plecoptera each contributing 10-20% (Ormerod 1987).

As a result of the low reliance on aquatic insects Ormerod and Tyler concluded that grey wagtails are less likely to be affected by stream acidification than other species of riverine birds. Abundances of aquatic invertebrates are significantly reduced in acidic streams compared with circumneutral streams but invertebrate abundance 5-10 m from the stream is not affected. The availability of a riparian food supply reflects bankside land-use, with broad-leaved woodland providing a greater abundance. The seasonal pattern of invertebrate biomass and size along streams in broad-leaved woodland habitat is most closely correlated to the breeding period of the grey wagtail. These factors may help to explain why they prefer wooded streams, despite foraging away from the trees themselves.

6.10 Warblers

6.10.1 Habitat summary

Reed warbler (*Acrocephalus scirpaceus*)

- Distribution See map (Figure 6.30)
- Climate Mean July temperature above 16 °C, rainfall below 1000 mm per annum or 75 mm July.
- Terrestrial vegetation First year: reed beds (*Phragmites*)
Second year: *Epilobium*, *Filipendula*, *Craetagus*.
- Nest sites 0.3-0.6 m above ground level, lower among *Phragmites*.
- Site fidelity Strong.

Sedge Warbler (*Acrocephalus schoenobaenus*)

- Distribution See map (Figure 6.31).
- Altitude Up to 350 m above sea level.
- Moisture regime Dry.
- Nest sites New reeds 0-2 m tall.
- Terrestrial vegetation Dense: herbaceous, bushes and brambles.
- Population density Maximum 5-6 pairs ha⁻¹

Marsh warbler (*Acrocephalus palustris*)

- Distribution See map (Figure 6.32): rare.
- Moisture regime Dry, but near water.
- Terrestrial vegetation *Urtica*, *Epilobium*, *Filipendula*.
- Nest sites Rarely over water. Historically osier beds (*Salix viminalis*) and almond willow (*Salix triandra*).

Grasshopper Warbler (*Locustella naevia*)

- Distribution See map (Figure 6.33)
- Moisture regime Historically: Damp (e.g. sedge fields, reedbeds, marshes)
Recently: Shift to drier habitats.

6.10.2 Introduction

Warblers are small insectivorous birds. Many are associated with trees or scrub but three members of the genus *Acrocephalus* are closely associated with wetland habitats; and a fourth of the genus *Locustella*, with damp meadows

6.10.3 Reed warbler (*Acrocephalus scirpaceus*)

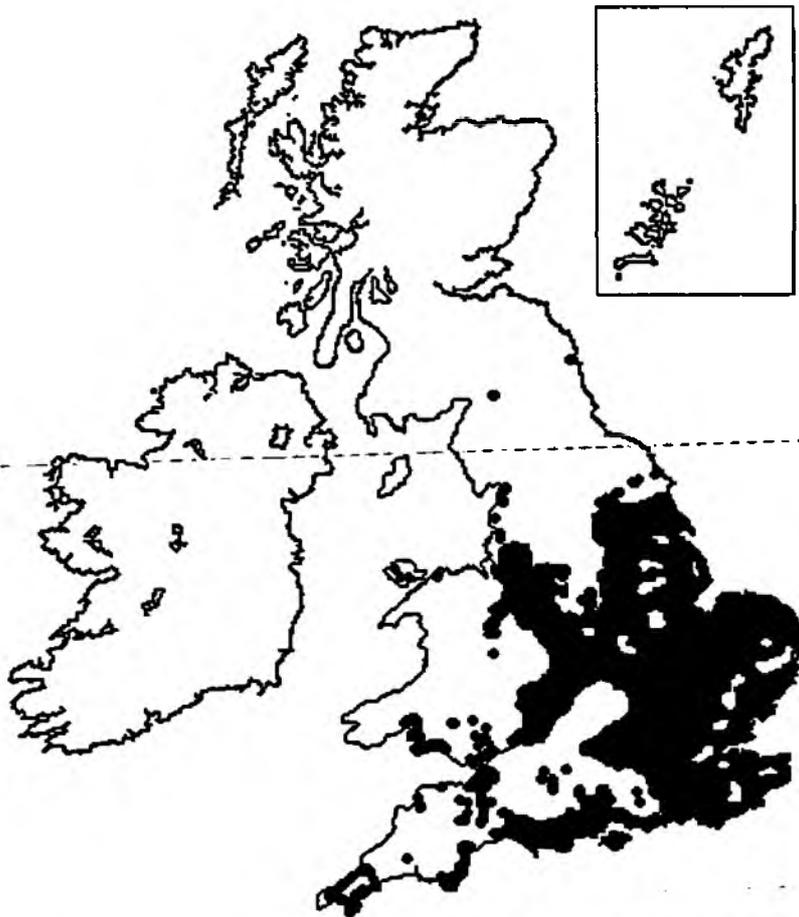


Figure 6.30 Broad distribution of the reed warbler in the British Isles (Sharrock 1976)

The basic habitat requirement for the reed warbler is reed beds (*Phragmites*), with a supplementary adjacent habitat of willowherb, meadowsweet and hawthorn. A comparison of the distribution of reed warblers and *Phragmites* shows a close correlation, *Phragmites* being concentrated to the south and east of a line drawn from the north Yorkshire coast to Start Point,

Devon. Although *Phragmites* occurs in localised stands up to south Shetland and throughout Ireland, this is not the case for the reed warbler; probably due to some quality factor of *Phragmites* in northern and western regions. The reed warbler is a migrant species which enters and leaves from the south-east, which offers an alternative physical explanation for the lack of colonisation as far west as Ireland.

There have been few records of reed warblers to the north of the 16°C July isotherm (July is their month of fledging). In addition, few reed warblers are found where rainfall exceeds 1000 mm per annum (or >75 mm in July), possibly due to the associated flattening of reeds and disruption of nests (Sharrock 1976).

The reed warbler is a monogamous species which constructs hanging nests amongst vertical vegetation. A well-grown *Phragmites* bed might support more than 10 pairs per hectare (Sharrock 1976). The recent loss of natural habitats has been mitigated by flooded gravel pits and other artificial water bodies. Reed warblers tend to return to areas close to where they fledged, with many adults breeding in the immediate vicinity of old nests. This behaviour is especially relevant given the longevity of the reed warbler compared to other passerine birds (3% aged 5-12 years); hence any habitat loss has a great impact upon the local reed warbler population (Anselin and Meire 1989).

The reed warbler exhibits a high degree of habitat selectivity. Habitat selection at the territory level is made by the male, but the choice of nest site within the territory is made by the female. One survey found that 54% of the recorded reed warbler nests were associated with *Phragmites* and the remaining 46% with other vegetation (Catchpole 1974: see Table 6.12).

Table 6.12 Percentage use of vegetation types by the reed warbler (Catchpole 1974).

<i>Phragmites</i>	54	Dryland habitats	20
Other Marshland Reedbeds	26	Mature <i>Salix</i>	2
<i>Glyceria</i>	8	<i>Rubus</i> (bramble)	1
<i>Typha</i>	2	<i>Rubus</i> (raspberry)	3
<i>Lythrum salicaria</i>	7	<i>Epilobium</i>	13
<i>Salix</i> saplings	5	<i>Filipendula</i>	1
<i>Rumex hydrolapathum</i>	3		
<i>Juncus</i> and <i>Carex</i>	1		

Catchpole (1974) found a highly significant difference between the number of vertical stems used as a support for the reed warblers' nest in *Phragmites* compared to other vegetation. Two advantages to nesting in *Phragmites* have been proposed: that the availability of supporting stems provide a more stable nest base; and that individual *Phragmites* stems are more rigid than average stems, making the whole system stronger (Catchpole 1974). The stems of *Glyceria* may be too thin and widely spaced (therefore prone to flattening) for strong colonisation. Other plants may become too thick before attaining a suitable height and rigidity for nest-building, such that the reed warbler cannot weave a suspension point around their stems.

The nest of the reed warbler is generally 0.3-0.6 m above the ground, although in *Phragmites* a higher proportion of nests are found at 0-0.3 m (Catchpole 1974). The high growth rate of *Phragmites* means that this plant can offer a variety of nest heights as the season progresses. *Phragmites* does not die down in the winter: dense growth in the spring may act as a cue in site selection, and the old growth may itself provide early nest suspension points.

The practice of burning back accumulations of dead *Phragmites* (and any associated invasive species) is detrimental to reed warbler nesting because no springtime cues for nesting

remain; there are no early nest sites in the form of dead stems; and there is a general decrease in the density of stems in the reedbed, reducing nest stability.

Nest failure is considerable, due mainly to egg predation which is greatest in pure, wet reed beds. The fragile nests often remain intact – Bibby and Thomas (1985) suggested that this indicates predation by the cuckoo, rather than by corvids or mustelids. The sites least susceptible to predation are not present, or not easily located, by early-arriving individuals. This is offset by the extended breeding season for early arrivals, which provides the opportunity for replacement clutches.

6.10.4 Sedge warbler (*Acrocephalus schoenobaenus*)



Figure 6.31 Broad distribution of the sedge warbler in the British Isles (Sharrock 1976)

The sedge warbler (*Acrocephalus schoenobaenus*) inhabits thick growth at the waterside, usually in drier habitats than the reed warbler (Sharrock 1976, Anselin and Meire 1986). In response to the increasing proportion of wholly dry habitats (e.g. forestry plantations, oil-seed rape and corn) the sedge warbler has begun to colonise artificial habitats such as gravel and clay pits.

Bushes and brambles appear to act as a nesting cue for sedge warblers returning in spring. The nests of the sedge warbler are generally found low down in dense vegetation,

favouring new reed growth of 0-2 m (Anselin and Meire 1989). In favourable habitat, the density of sedge warblers can reach 5-6 pairs per hectare, though such areas are limited. Farmland plots support an average density of 1.3 pairs km⁻² (Sharrock 1976). Bushes which are used as songposts may be important features in landscapes of uniform, low vegetation.

Sedge warblers are found throughout England and Wales – in one study the sedge warbler was recorded in 76% of 10-km squares surveyed, compared with 20% for the reed warbler (Sharrock 1976). The sedge warbler is scarce at high altitudes (e.g. Pennines, Wales, Devon, Scottish Highlands) although it is known to breed at altitudes up to 350 m above sea level if suitable habitat is available. According to the Common Birds Census, there was a sharp population crash in 1968, with slow recovery thereafter (Sharrock 1976).

6.10.5 Marsh warbler (*Acrocephalus palustris*)



Figure 6.32 Broad distribution of the marsh warbler in the British Isles (Sharrock 1976)

The marsh warbler is closely related to the reed warbler, but is much less common and is protected under Schedule I of the Wildlife and Countryside Act 1981 (Kelsey 1989). Britain is on the western edge of its range. Marsh warblers arrive late in the season, usually after late May; and also leave early, usually by mid-August (Sharrock 1976).

The marsh warbler is often found in the same general areas as reed and sedge warblers, nesting close to water in dry areas. The majority of nests are found attached to stems of nettles, meadowsweet or bushes, with few being located over water. Historically, osier beds (maintained for basket-weaving material) provided an important habitat. The almond willow which was commonly found in such beds regularly carried nests, where the stems of 2-3 year old trees were probably preferred for nest suspension. The marsh warbler has a mimetic song pattern, with over 50 bird species being imitated (Walpole-Bond 1938).

The number of marsh warblers has decreased over the past 40 years, probably as a consequence of drainage and the loss of osier beds, which if left unmanaged develop into wet woodlands. The most important population is centred in the west midlands of England, though this is diminishing. Breeding in Herefordshire and Gloucestershire was last recorded in 1954 and 1984 respectively. In Worcestershire, there were about 95 pairs in the 1960s; 38-60 pairs in 1976; and 3 pairs with one unpaired male in 1987 (Sharrock 1976, Kelsey 1989).

6.10.6 Grasshopper warbler (*Locustella naevia*)

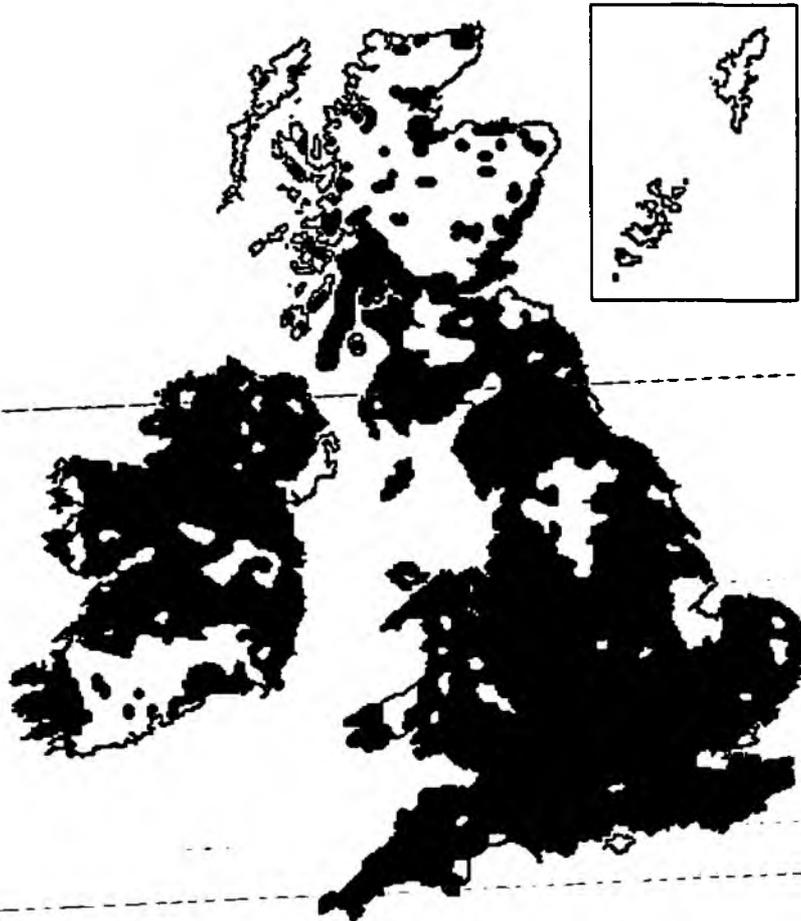


Figure 6.33 Broad distribution of grasshopper warbler in British Isles (Sharrock 1976)

Water is not a prerequisite for the grasshopper warbler – as well as in damp sedgy fields, reedbeds and overgrown marshes, it is also found on down and heathland and Sharrock

(1976) suggested that drier habitats have become prevalent. Recent coniferous afforestation has provided a wealth of dry tangled grass, willowherb and brambles in the early stages of its cycle, which has mitigated the loss of natural wetland sites. In a young plantation, grasshopper warblers breed at a density of about 0.3 pairs per hectare; whilst on chalk, grassland scrub there are typically less than 0.2 pairs per hectare (Sharrock 1976).

This bird is absent from most of upland Britain. Migrant grasshopper warblers arrive in the south of this country by the end of April. In 1976, the estimated population of grasshopper warblers in Britain and Ireland was about 25 000 pairs (Sharrock 1976).

6.11 Snipe (*Gallinago gallinago*)

6.11.1 Habitat summary

- Distribution See map (Figure 6.34).
- Moisture regime Damp, penetrable soils: rushy fields, water meadows, washes, blanket bogs and salt marshes.
- Terrestrial vegetation Tall.



Figure 6.34 Broad distribution of the snipe in the British Isles (Sharrock 1976)

6.11.2 Introduction

The snipe is a ground-nesting wader, usually on rushy fields, water-meadows, washes, blanket bogs and salt marshes, and occasionally on dry meadows and moorland. It feeds mainly upon earthworms and Diptera larvae, probing with its long bill (Green 1988). Progressive drainage of bogs and marshy grassland has led to a general decline of European snipe numbers (Sharrock 1976).

6.11.3 Breeding

The onset of breeding is determined by photoperiod, weather conditions and food availability. Spring weather may affect the timing of nesting indirectly, due to reduction of ground-space by flooding and interference with feeding. Snipe chicks hatch during a broad period from mid-May to August.

Green (1988) found failure of about 40% of nests: due to predation (60%), trampling (20%), flooding (10%) and desertion (10%). The predation risk decreases through the season but this is balanced by an increased risk of trampling. Predation risk does not seem to be strongly correlated with the height of grass (available cover) and may be due to a shift in the predators' dietary preference. After hatching, the brood is divided between the parents and forages as two separate units (up to 100 m apart), probably reducing the impact of predation. The chicks fledge at 3 weeks and achieve adult proportions after another month (Sharrock 1976).

During winter, snipe mainly feed at night and roost by day in 'forms' hollowed out of long grass or vegetation – this activity pattern continues for the males throughout the breeding season. Snipe nests are continuously incubated during the night but the male takes no part in incubation, and nests are briefly abandoned during the females' diurnal feeding. The female can only leave the nest for brief periods (totalling about 22%) and so the presence of good foraging sites close to the nest is important (Green *et al.* 1990). By feeding in surrounding meadowland the female remains better-hidden than along the open-vegetation of ditch edges, which are often bordered by sparse vegetation.

Nesting is sustained for the longest time where soils remain penetrable, such as areas of poor drainage or intentional maintenance of water levels. Following drainage for agriculture in the Netherlands (1940-1980s), the time of first sightings of snipe chicks changed little but the season finished earlier (Beintema *et al.* 1985). In England and Wales, land drainage intensified during the 1960-70s, which may be a cause of the recent reduction in lowland snipe breeding populations. Prolonged surface flooding of meadows during the spring and summer may be equally detrimental to snipe, by affecting earthworm populations (Green *et al.* 1990).

Snipe are inconspicuous when feeding, incubating and rearing their young, except when the males (and sometimes females) perform display flights with a 'chip-per chip-per' call and 'drumming' vibration of the outer tail feathers (Sharrock 1976, Green 1985). Green (1985) suggested that surveys made by walking a site, noting birds heard or seen, might underestimate the breeding population. Drumming activity varies with time of day, stage of incubation and weather conditions: maximum activity occurs for a short period on either side of dawn and dusk; in damp weather; or in response to disturbance (Sharrock 1976). Snipe may also display whilst passing through an area on migration, corrupting the population estimate for that locality.

6.12 Common Sandpiper (*Actitis hypoleucos*)

6.12.1 Habitat summary

- Distribution See map (Figure 6.35).
- Gradient Middle reaches of upland rivers, 2-33 m km⁻¹
- Flow regime Riffles.
- Feeding habitat Shingle shorelines. Estuaries, tidal mudflats and sewage works, during migration.
- Nest site Within 300 m of water.
- Terrestrial vegetation Coarse, grassy. Open canopy.
- Nest spacing At least 18 m
- Population density Maximum 5 pairs km⁻¹. Average : rivers 0.57 pairs km⁻¹; reservoirs 0.73 pairs km⁻¹
- Disturbance Sensitive: avoids footpaths and anglers.

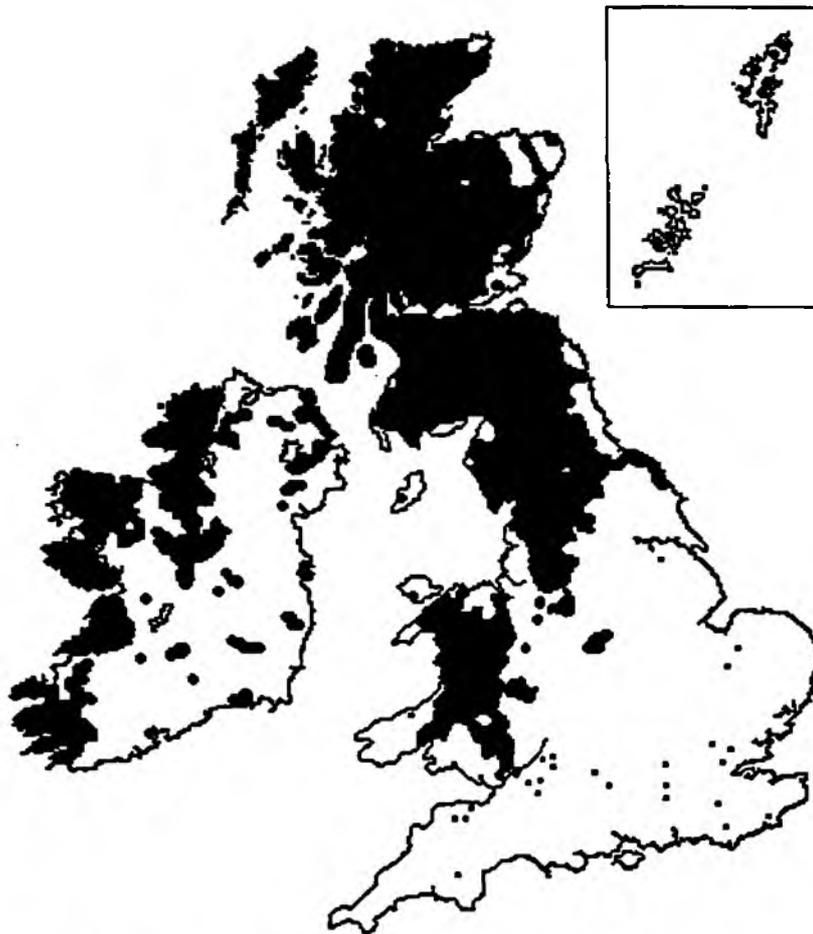


Figure 6.35 Broad distribution of common sandpiper in the British Isles (Sharrock 1976)

6.12.2 Introduction

The common sandpiper is a wader, in Britain characteristic of upland streams and rivers. The species has a number of diagnostic features, especially the bobbing motion of head and tail (similar to wagtails) at the waterside. Whilst the bird is stationary, the white underparts and brown upperparts clearly contrast; and in flight it shows white wing bars, a dark rump and a characteristic flight across water surfaces with drooping wing tips, tending to call with a high rapid trill.

According to Sharrock (1976) the summer population of perhaps 50 000 pairs is largely confined to northern upland streams and reservoirs – western Ireland, Scotland, northern English uplands as far south as the Peak District, and mid/north Wales. Small numbers overwinter on the estuaries and flood plains of southern and western England, but most migrate to Africa (Cramp and Simmons 1983).

6.12.3 Courtship

The territory of the common sandpiper is usually linear, following a river or the shoreline of a reservoir. Territory establishment takes place in late April to early May, on arrival from wintering grounds. The courtship display usually consists of a circling flight upwards over open water, combined with loud trilling, and is mainly performed by territory-holding males. Potential mates may also closely chase each other in close formation. On narrow, wooded streams the flight is modified, flying to a particular physical feature then returning in tight loops. The display flights usually last 2-4 minutes and may be directed at the settled female by the male. Other displays are carried out on the ground in sufficiently open areas, such as bankside grassland or shingle areas. These include holding up one or both wings to potential mates, to expose the white flank beneath whilst calling.

6.12.4 Breeding

The breeding-season of the common sandpiper is extremely short – perhaps timed in order for chicks to be able to exploit the rich aquatic food source at the end of June (see later), whilst tying the adults to the breeding territory for the least possible time. Males arrive and establish territories around mid-April and by mid-July adults and juveniles leave the breeding grounds to migrate.

The territories established during breeding are usually well-defined but sometimes overlap. The most usual breeding density along rivers is 0.57 pairs km⁻¹ and on reservoir shores 0.73 pairs km⁻¹ although there can be 1-5 pairs per kilometre of shore and the shortest documented nest spacing is 18 m (Holland *et al.* 1982a, Cramp and Simmons 1983).

The most important factor affecting sandpiper density appears to be the proportion of shingle in any stretch: sites with riffles and areas of exposed shingle can support more pairs. Comparing various characteristics of three Welsh rivers and their waterbird populations, Round and Moss (1984) found that the only feature which correlated with common sandpiper density was shingle. Shingle areas and riffles are most abundant in the middle reaches of upland streams. In the upper reaches of such streams, shingle and gravel are often mobile, whilst finer sediment tends to predominate in the lower reaches. Nesting in Peak District streams is associated with a gradient of 2-33 m km⁻¹. In Scotland, Cuthbertson *et al.* (1952) concluded that streams steeper than 38 m km⁻¹ were avoided.

It is generally agreed that nests are usually found within 300 m of the waters edge; some nests may be sited at the waters' edge, especially on islands, but these are often flooded. The

nest is usually on the grassy verge of shingle banks (especially at reservoir sites), or at the edge of a clump of vegetation near to the water course (Cuthbertson *et al.* 1952, Holland *et al.* 1982a, Cramp and Simmons 1983, Yalden 1985). The nest itself varies from a 'cup' to a single scrape, lined with vegetation and debris, often with vegetation pulled over the top and front for concealment (Ratcliffe 1990).

Incubation by both adults lasts for 21-22 days. The non-incubating parent roosts partially concealed, 60-80 m away. Slight weight loss in adult birds during the breeding season may be a consequence of concentration on egg protection at the cost of feeding (Holland *et al.* 1982b). Increased availability of aquatic and terrestrial insects at the end of their breeding season allows sufficient weight gain for subsequent migration.

Hatching success is very high. Cuthbertson *et al.* (1952) and Holland *et al.* (1982b) estimated 80% and 89% success respectively, while Cramp and Simmons (1983) cited 84.7% success from a study made in the USSR. This is greater than for other waders such as the Curlew (46.5%) or Lapwing (54%).

The young are led to an area where they will be able to feed whilst close to cover. Initially they may be kept in coarse vegetation until they can move quickly enough to feed in open areas and run for cover. Young birds feed within the territory until they fledge at around 2.5-3 weeks of age. Holland *et al.* (1982b) estimated fledgling success at only 35%, but adult survivorship is up to 80% per annum.

6.12.5 Diet

The common sandpiper's diet is quite general, with a large range of invertebrate animals being taken (Cramp and Simmons 1983: see Table 6.13, Yalden 1985). During migration a number of habitats are exploited as feeding areas, such as estuaries, tidal mudflats, sewage works and open pasture.

Table 6.13 Dietary items of the common sandpiper (Cramp and Simmons 1983)

Coleoptera (e.g. Carabidae, Curculionidae, Hydrophilidae, Dysticidae, Scarabaeidae, Chrysomelidae)	Dermoptera (<i>Forficula</i>) Acrididae and Gryllidae Plecoptera Ephemeroptera	Araneae Mollusca (e.g. <i>Hydrobia</i> , <i>Littorina</i> , <i>Planorbis</i>)
Diptera (e.g. Tipulidae, Culicidae, Tabanidae, Muscidae, Stratiomyidae)	Trichoptera (e.g. Phryganeidae) Lepidoptera (e.g. <i>Aglais</i>) Crustacea (e.g. <i>Talitrus</i> , <i>Gammarus</i> , <i>Carcinus</i>)	Annelida (Lumbricidae, Nereidae) Amphibia: small frogs and tadpoles (e.g. <i>Rana</i>)
Hemiptera (e.g. <i>Gerris</i> , <i>Corixa</i>)		Small fish

Although breeding is largely restricted to riparian habitats, the diet of the adult continues to be generalised, composed largely of non-aquatic items. Yalden (1986) found that 74.4% (of sandpipers examined) had taken terrestrial food such as ants, spiders, earthworms, weevils, and carabid beetles. Early in the season, adults were foraging in fields close to the riparian zone: this became less evident as the season progressed and grass height increased. They also exploited the grassy edge of the stream bank and the shingle/boulder margin of the channel.

Juvenile birds (Yalden 1986: observed for 8-9 hours) had similar feeding regimes to adults, but there was a major difference between the feeding habitats exploited by different age classes. Young chicks (0-5 days old) mainly foraged in short bankside grass, whilst older chicks moved to the waterside gravel and shingle beds. Yalden suggested that feeding behaviour might be the main control of habitat selection during the breeding season.

Holland *et al.* (1982a) found from faecal and pellet samples that aquatic components of the diet are not necessarily dominant. However, numbers and biomass of benthic macroinvertebrates are high during the sandpiper breeding season and Yalden (1986) suggested that this may be important for survival of older chicks. In order to fledge each chick needs to gain approximately 32 g in 20 days, requiring an easily accessible and energy rich food.

6.12.6 Predation

Little is known about predation of common sandpipers. Cuthbertson *et al.* 1952 suggested the loss of at least two study nests was attributable to carrion crows; a ubiquitous species which would probably be present in any sandpiper habitat. Predation is also documented on sandpiper adults by peregrine falcons in parts of Scotland (Ratcliffe 1990) and individuals have been observed to adopt a freezing posture when aware of the presence of a hunting sparrowhawk (Dougal *et al.* 1987). It must be assumed that other predatory birds and mammal species present a risk.

6.12.7 Human influence

Whilst on migration this species often stops at 'staging posts' in order to feed; in Britain, favoured areas are often sewage farms.

Holland *et al.* (1982a) proposed that:

'... the high riverine population along the Alport and Ashop rivers is also probably correlated with their privacy and the absence of riverside paths. It is notable that the one stretch of the river Ashop which has a riverside footpath, near the confluence with the Lady Clough, has never had any sandpiper territories although in every other respect the area seems entirely suitable'

These workers also noted a reduction in breeding population along the upper Dove and Blake Brook, and inferred that this may have been due to the construction of small weirs (and therefore pools) by anglers which preclude the shingle areas important to sandpipers. Absence of territory-holding birds could also be due to repeated disturbance.

Yalden (1984) noted that since its breeding and incubation period falls in late May and June, the Derwent Valley population is vulnerable to recreational disturbance, especially around the spring bank holiday. He found that peak use of the area (using counts of parked cars) occurred then, rather than the height of the holiday season in late summer. The distribution of sandpiper territories varied between years, apparently corresponding with recreational pressure through variation of walker's access and suitability for angling.

The afforestation of upland areas changes the habitat characteristics and may increase predation of ground nesting birds (Usher and Thompson 1988). This has been especially clear in areas of the Flow Country of northern Scotland, where breeding populations of many waders have declined. Most research effort, however, has targetted other birds such as plovers (Ratcliffe 1990).

The common sandpiper appears to be little affected by the acidification of many of its home streams (Vickery 1991), perhaps due to the importance of aquatic food supplies only during a small period of the breeding season.

6.13 Little Owl (*Athene noctua*)

6.13.1 Habitat summary

- Distribution See map (Figure 6.36): pasture and meadows, old orchards and associated parkland, drained fenland lined with pollarded willows.
- Altitude Lowland, not above 600 m
- Diet Omnivore: invertebrates, amphibians, reptiles, birds and mammals.
- Terrestrial vegetation Avoids dense stands of trees or other vegetation.
- Nest sites Tree holes (e.g. *Quercus*, *Fraxinus*, *Salix*, *Prunus*) 3 m (0.3-12.2 m) above ground level; about 20 cm wide and 80 cm deep.
- Nest spacing Minimum 240-320 m
- Territory size About 35 ha (water meadows, mixed farmland)

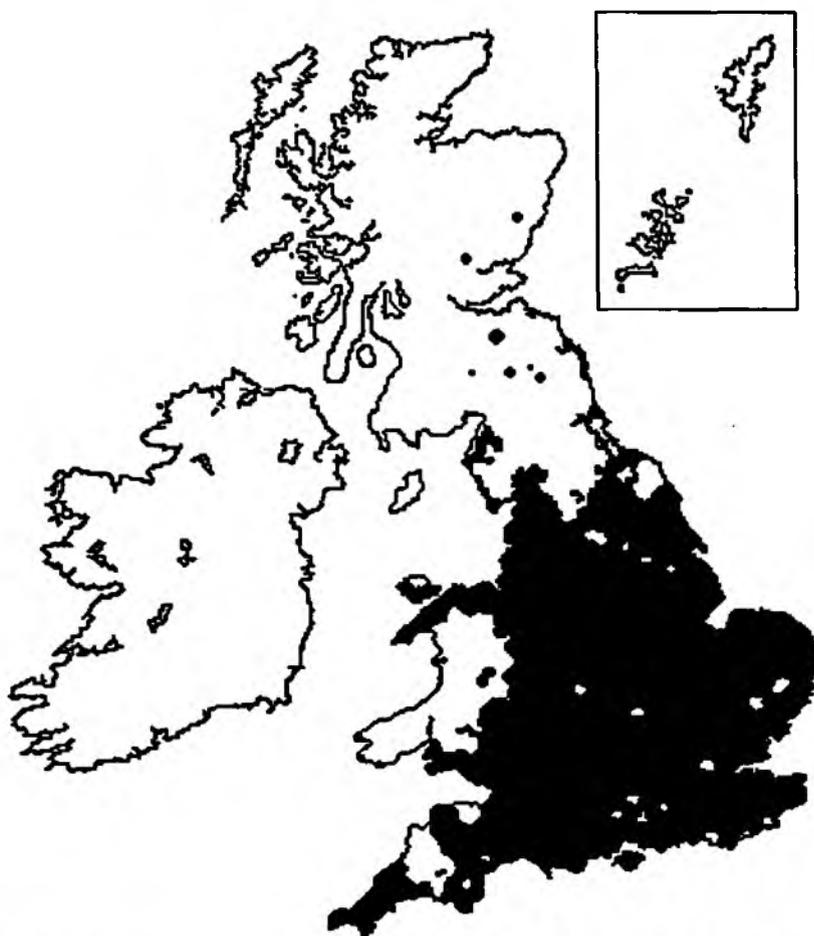


Figure 6.36 Broad distribution of the little owl in the British Isles (Sharrock 1976)

6.13.2 Introduction

The little owl has a small body with a plumage of varying colour (grey - rufous brown - ochre - buff). It is not a forest species, avoiding tall, dense stands of trees and other vegetation; preferring open landscapes with conspicuous look-out posts from which it can make short, low daytime flights. Little owls are generally found in lowland areas such as pastures and meadows (≤ 600 m above sea level) with year-round short herbs (Finck 1990). The little owl is not an indigenous species: in the late nineteenth century releases occurred in several counties and by the end of the nineteenth century it was breeding regularly in Kent, Bedfordshire, Northamptonshire and Rutland. Continued introductions produced a rapid expansion of the little owl population. By 1920, every county south of the River Humber supported the little owl, except parts of Wales and south-west England, and the population size peaked in the early 1930s. The numbers of little owl dropped between 1940-60 (possibly as a result of pesticide bio-accumulation) and is now markedly scarcer in the south of England (Sharrock 1976).

6.13.3 Site selection and territory

The little owl often nests in tree-holes, but recently its British habitats have included agricultural areas with hedgerows and old farm buildings, old orchards and their associated parkland, and the pollarded willows of drained fenlands. The little owl perhaps competes for food and nesting sites with the tawny owl (Sharrock 1976). The main threats to the Little owl population come from intensive agriculture with its associated tree-felling, demolition/repair of outbuildings, use of toxic chemicals and increased disturbance.

There is limited information available on social behaviour of the little owl. Out of the breeding season the little owl is either solitary or is found in pairs. Yearlings may breed, and will form monogamous pairings which may last for up to 4 years. In the south of England, the average territory size is 35 ha in water-meadows, 38 ha in mixed farmland with a minimum inter-nest spacing of 240-320 m (Glue and Scott 1980: cited by Cramp *et al.* 1985). Some individuals maintain territories throughout the year, but territorial behaviour and territory size vary seasonally (Finck 1990, see Table 6.14).

Table 6.14 Seasonal variation in territoriality of the little owl (Finck 1990)

Season	Circumstances	Behaviour and territory size
Spring	Increasing food availability. Courtship begins.	Peak in male aggression. Territory as large as defensible.
Breeding season	Foraging increases for mate and chicks.	Male distracted, territory size reduced.
Summer	Offspring sharing territory. Poor feeding conditions, moulting.	Males in worst condition. Smallest territory size.
Autumn	Food density and accessibility increased. Preparing for winter resource depression. Young-of-year establishing territories.	Male aggression returns. Territories expand.
Winter (snow cover)	Foraging easy. (Feeding difficult, decline in body size)	Territory as springtime. (Territoriality falls, territory contracts)

6.13.4 Breeding

The little owl favours oak, ash, fruit and willow trees for nest sites, in that order of frequency, with cavities 0.3 - 12.2 m (mean 3.0 m) above ground level (Glue and Scott 1980: cited by Cramp *et al.* 1985). The site of the nest within the tree may vary: it is most often in the main trunk but lateral branches or pollards may be used. The chamber of the nest cavity is

sometimes cleared, but no extra material is added. Glue and Scott found that the mean cavity width was 20 cm; and the mean depth of the passage 80 cm.

Clutch sizes vary from 1-7 eggs, with 3-4 eggs in 75% of the clutches recorded by Glue and Scott (1980). The female incubates the eggs for 27-28 days, aggressively defending the nest, whilst the male obtains food. The hatchlings remain dependent upon the parent birds for up to a month after fledging.

First-year birds vacate their nests sites and may continue dispersing beyond late autumn, however, they tend to remain in the vicinity of their natal sites. Cramp *et al.* (1985) found that most settled within 20 km, though a small proportion of ringed birds were recovered over 20 km (extremely 150 km) from the original nest site.

6.13.5 Diet

Prey items range in size up to a half-grown rabbit (Sharrock 1976), including small mammals and birds, reptiles, amphibians and invertebrates (e.g. Coleoptera, Orthoptera, Dermaptera, Lumbricidae). The little owl forages from dusk until midnight, resting for a few hours and then continuing until dawn. The average hunting area for a little owl is about 0.5 km². The owl uses a variety of hunting strategies – swooping from look-out perches, flying after insects through the air and also searching on the ground for invertebrates. The average individual daily food requirement is 50-80 g. The diet varies seasonally: birds, Tipulidae and Dermaptera are most important in May-July, August-November and autumn/winter respectively; whilst invertebrates as a whole are always a significant food resource. Invertebrates are particularly important to young birds.

7. MAMMALS

7.1 Background

About one hundred species of mammals have been recorded in the British Isles, of which the majority are marine or wholly terrestrial. Many of those which are aquatic, or associated with river corridors, are important indicators as a result of their need for mixed habitat types or feeding areas; good examples are the bat species. The distribution and activity of some mammals, such as the otter, can be assessed without direct observation.

The otter, water vole, water shrew, mink, and four bat species are reviewed here.

7.2 Otter (*Lutra lutra*)

7.2.1 Habitat summary

- Distribution See map (Figure 7.1)

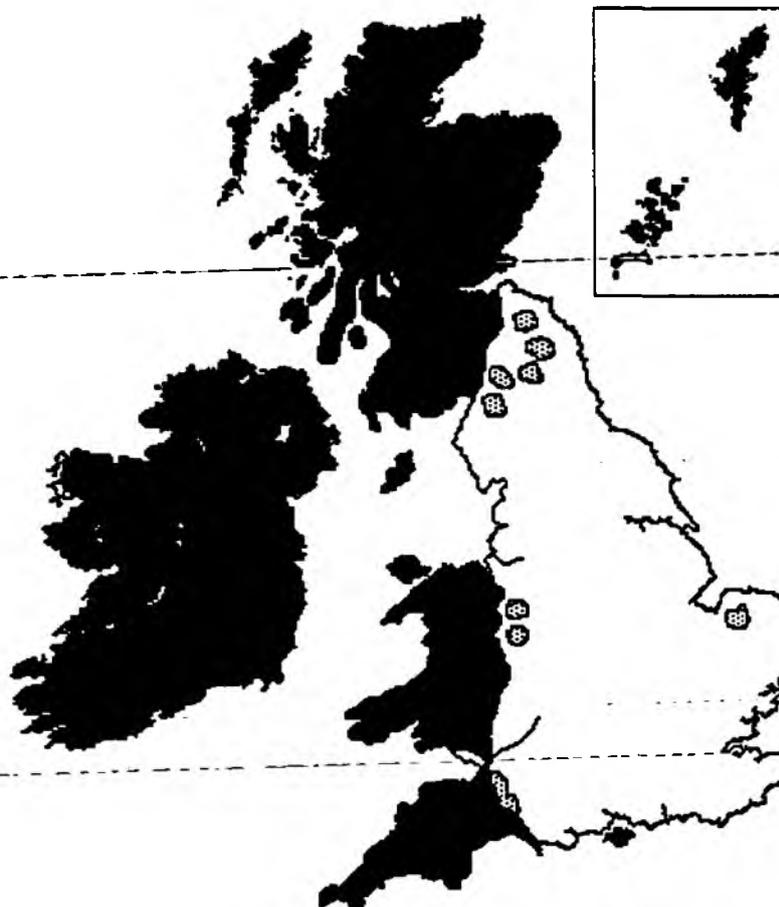


Figure 7.1 Distribution of the otter in the British Isles (Foster-Turley *et al.* 1990)

- Terrestrial vegetation Couch sites, more than one per kilometre - dense, low scrub (hawthorn, blackthorn, gorse, bramble, bracken)
- Water chemistry Avoid acidic runoff (i.e. from coniferous forest)
- Territory size Male c. 19 km, female c. 8 km
- Holt locations Eroded tree-root systems (e.g. of oak, sycamore, ash)
- Number of holts Many - around thirty.
- Human disturbance Sensitive nocturnally.

7.2.2 Introduction

The Eurasian otter has one of the widest distributions of all Palaearctic mammals (Chanin and Jeffries 1978). It is usually found in freshwater but strong populations exist on the Scottish islands and west coast. It feeds largely on fish; may breed throughout the year; requires undisturbed holts within its territory; and is generally sensitive to human disturbance. A severe population decline has occurred over the past thirty years.

7.2.3 Diet

An aquatic carnivore, the otter has a fairly catholic diet with a wide range of prey form and size (Figure 7.2).

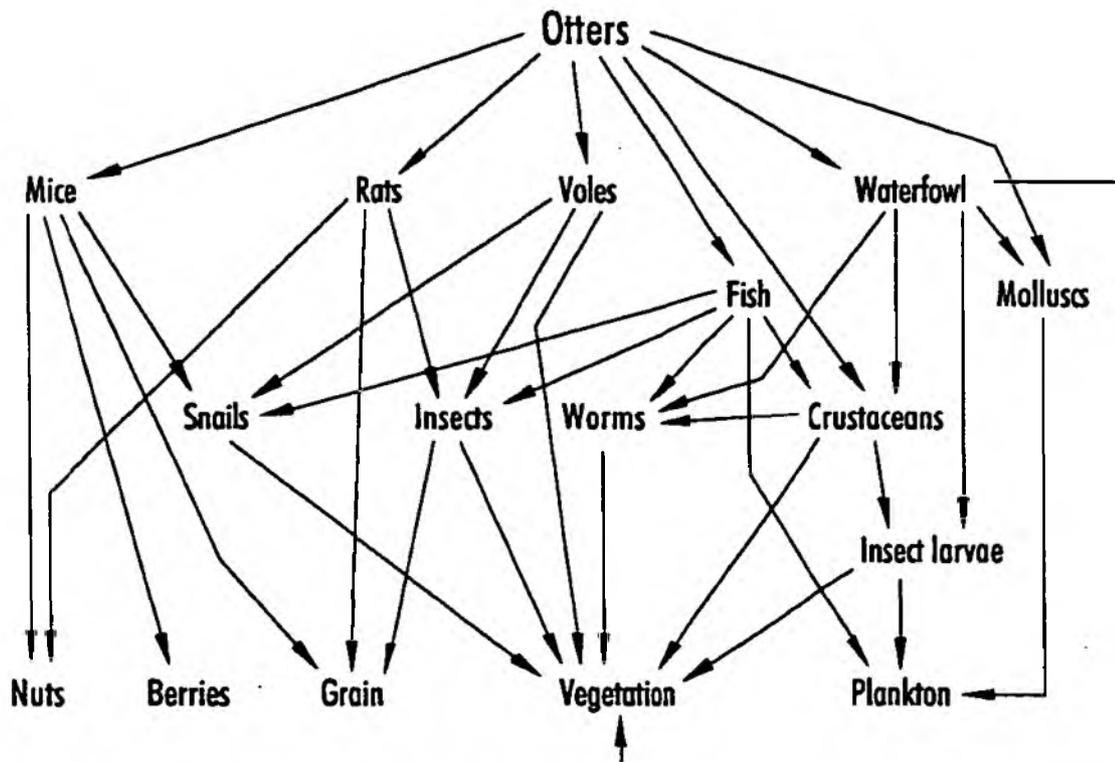


Figure 7.2 Food relationships of the otter

The composition of the diet is largely decided by availability: as a general rule, whatever food items are most abundant in the habitat will form the main dietary constituent. The otter is not a wholly indiscriminate predator and may select against abundant species if they are less palatable (e.g. Erlinge 1967a - zander and tench in Lake Sövdeshön, central Scania). Some studies have found definite seasonality of the diet, again linked to changing availability. Fish are a consistently important component of the diet (Fairley and Wilson 1972a, 1972b, Weir and Bannister 1972), with slower-moving species taken more often.

7.2.4 Territory

Otters usually maintain fixed territories, with the boundaries marked by deposits of scented faeces ('scats' or 'spraints'). These olfactory signals seem to serve a solely territorial purpose. Whilst there is no change in the frequency of spraints during the rutting season, sprainting activity has been seen to increase during times of high population density, in response to increased pressure on the territory boundaries (Erlinge 1968). The territory size of a dog otter varies with its position in the social hierarchy and with the associated terrain. In general, the home range and territory size of a dog is approximately twice that of a female with her associated cubs (Erlinge 1967b). Estimates of territory length have been 19 km for males and 8 km for females (King *et al.* 1976); and 4-5 km (Erlinge 1968). There are areas of concentrated activity at the centres of otter territories, with pathways radiating out from them. These centres tend to be areas of cover (dense vegetation) with least disturbance.

Certain types of vegetation, or cavities, situated close to the water, can be used as dens, or 'holts'. Individuals have been found to use up to 29 holts (Andrews 1989). Female otters move their cubs from the natal holt, which is removed from the main centres of activity, to secondary holts. Evidence of cubs in a holt does not therefore indicate that the surroundings constitute a complete otter habitat (Taylor and Kruck 1990). Potential holts can be subdivided into two broad categories, surface and sub-surface.

Surface holts or 'couches' are made from dense vegetation about 0.5 m tall, which is inaccessible to livestock (Mason and Macdonald 1986). The mean distance between couches is about 1.5 km; but they tend to be clustered around sites of otter activity and the otter may become more susceptible to disturbance if the density of good resting sites falls below one per kilometre (Macdonald *et al.* 1978). Couches are found in aggregations of woody debris; scrub vegetation such as hawthorn, blackthorn, gorse; and bramble thickets or dense willow. Herbaceous vegetation such as bracken and Japanese knotweed may also prove suitable as temporary summer couch sites (Andrews 1989).

Sub-surface holts are cavities beneath the roots of mature trees or in banksides, constructed within the root systems of suitable trees such as oak, ash and sycamore. These trees have roots which grow out from the bank almost horizontally, forming cavities between themselves and the bank/water (Macdonald and Mason 1980). Less suitable trees are those with a fibrous root system such as alder and willow, which produce an impenetrable mesh in comparison to the more bulky systems of species such as oak. In a study of rivers in Wales and the west Midlands of England, ash and sycamore formed 50% of potential holt sites. A significant relationship between sprainting intensity and these two tree species was found, even when holt availability was removed from the ensuing factor analysis. This indicates an additional element in their selection - which might be that the root systems and their often-associated pools attract fish, thereby providing food for the otters (Macdonald and Mason 1983). The relative importance of adjacent woodland is equivocal: some studies have considered it important (Bas *et al.* 1981, Macdonald *et al.* 1978); whilst others have stressed the value of riparian cover, with adjacent woodland being less significant (Macdonald and Mason 1983).

In addition to holts, otter territories usually include several other features (Erlinge 1968):

1. Rolling places, at which otters dry and groom themselves, are usually situated very close to water at undisturbed sites. The activities of the otter, leaving scent on the ground, tend to rub out a smooth patch in the undergrowth of approximately 1 m².
2. Slides are runs of smoothed ground along which the otter can slide.
3. Feeding places, the sites of which depend on local food availability.

7.2.5 Decline of otter populations

A dramatic decline in otter numbers was recorded across Britain in the late 1950s. A number of potential causes have been suggested (Table 7.1), of which the use of persistent organochlorine pesticides such as Dieldrin has been most supported.

Table 7.1 Possible contributing factors to the decline of otter populations.

Potential cause	Notes
Direct killing (hunts, accidents)	No figures available, countrywide increase unlikely.
Disturbance	Detrimental, but variable through the otter's range.
Severe winters	Cold 1962-63 cited by Mammal Society (Anon. 1969); and harshest conditions co-incident with sharpest decline; but decline began before 1962-63.
Mink as disease vectors (e.g. distemper)	Otter decline pre-dated the main spread of mink.
Mink as competitors	As above, and they co-exist in North America (Hewer 1974)
Habitat destruction	Engineering and riparian clearance are certainly harmful, but no specific correlation with decline.
Chemicals (e.g. organochlorines, PCBs)	Well-documented impact on British wildlife in mid-1950s, especially on top predators (through bioaccumulation)

Since the introduction of legal constraints on the use of persistent chemicals, other predators such as sparrowhawks and peregrine falcons have recovered. A similar recovery of otter populations has not yet occurred, despite the fact that contemporary levels of pesticide residues do not seem to be a significant threat (Macdonald and Mason 1983). Although there have not been strong correlations between otter numbers and factors such as disturbance or habitat degradation or disturbance, they have been recognised and targeted for improvement.

The territory requirements of otters are extensive, making the provision of significant areas of suitable habitat a prerequisite for their effective conservation. In 1977, the Otter Haven Project (OHP) was jointly set up by the Vincent Wildlife Trust and the Fauna and Flora Preservation Society. The aim of this initiative was to identify river stretches where otters are resident, and then negotiate with the landowners for sympathetic management techniques ('haven' status).

The otter was added in 1978 to Schedule I of the Conservation of Wild Creatures and Wild Plants Act 1975; the effect of this was to make it illegal to kill, take or injure an otter without a licence. Initially, Scotland and Northern Ireland were exempt from this legislation due to their thriving otter populations. Due to declining otter numbers across Europe, these regions are now of international significance for the otter, and protection was extended by the 1981 Wildlife and Countryside Act.

7.2.6 Factors restricting otter distribution

Feral mink have been suggested as a barrier to otter population recovery; due to the transmission of disease and interspecific competition for food resources. There is no evidence that mink are significant vectors of diseases such as distemper which might affect the otter. Erlinge (1972) found a highly significant difference between the diets of mink and otter in Swedish lakes. A conflict should only occur in already stressed areas or seasons where mink, the more generalist feeders, will tend to be at an advantage.

Intense otter sprainting has been found along rivers subject to considerable organic pollution, but with potential holt sites (Macdonald and Mason 1983). The otter may not rely upon good water quality *per se*, but as a top predator it is vulnerable to bioaccumulation of persistent toxic chemicals such as organochlorine pesticides. There are some continuing potential sources of toxins; such as the use of dieldrin during mothproofing in the wool industry. Additionally although the otter's dietary requirements are plastic enough to incorporate small shifts in the availability of fish, a large depletion of fish stocks by any pollution (e.g. acidification) might be significant.

The level of disturbance from human activity (to a degree) is not significant so long as secure refuges are available (Macdonald *et al.* 1978), especially where human activity is restricted to the daytime (Macdonald and Mason 1983).

Although not the initial cause of the otter's population decline, habitat degradation may since have rendered many environments unsuitable for colonisation. Intensive post-war land drainage, with straightening and deepening of river channels, involved a widespread loss of riverside vegetation and physical diversity. No direct effect on otter populations can be demonstrated, but it is clear from River Corridor Surveys that many lowland rivers no longer contain the density of otter holt sites necessary to support a viable population.

7.2.7 Conservation management

The otter's decline has produced isolated populations with little or no communication between them, therefore more susceptible to any perturbation. Reintroduction and restocking of otter populations is controversial. Active reintroduction may be desirable (or a moral obligation) in areas which have become solidly isolated from remaining communities; but restocking is probably only a worthwhile option in the face of genetic problems, rather than habitat inadequacy.

Prime holt sites tend to be eroded root systems, which can conflict with the requirements of low-maintenance solutions to flood defence. Nevertheless, a positive policy to retain riparian tree cover is required. Bankside clearfelling is costly (c. £ 1250 km⁻¹ in 1978: Macdonald *et al.* 1978), and has side-effects which increase the maintenance requirement: reduced shading and increased nutrient loading enhance the growth of riparian and aquatic vegetation, which in turn increases the need for dredging, mowing or herbicide application. Coppicing of suitable trees to reduce their size and increase their stability, together with placement of instream current deflectors to counter erosion (Lewis and Williams 1984), provides a more elegant solution for both flood defence and conservation.

Artificial holts can be successful within dispersal distance of established populations, in areas fulfilling the basic requirements of *L. lutra* (e.g. low disturbance, clean water, vegetative cover). Several 20-cm diameter pipes can be used to form tunnels, leading from above or below water level, into a main chamber of 0.75-1 m³ (Lewis and Williams 1984). This chamber is usually constructed from breeze blocks or unmortared bricks and paving stones, with the roof waterproofed by polythene sheeting (Wood 1979).

7.3 Water vole (*Arvicola terrestris*)

7.3.1 Habitat summary

- Distribution See map (Figure 7.3)



Figure 7.3 Distribution of the water vole in the British Isles (Corbet and Harris 1991)

- Terrestrial cover Forb layer – high density of mixed species.
Tree layer – low density.
- Terrestrial vegetation Typically nettles, Scottish dock, redshank, amphibious bistort, brome, meadow foxtail, annual meadow-grass.
- Aquatic vegetation Common reed (*Phragmites*) and also soft rush, branched bur-reed, reed sweet-grass, reed canary-grass, reedmace.
- Geology Calcareous, base-rich.
- Soil type Loam, sand.
- Bank height Usually over 1 m; at least 0.5 m
- Bank slope and nature More than 35°, undermined.

• Water depth	Up to 75 cm
• Substrate	Muddy.
• Stream width	1-3 m
• Current velocity	Generally less than 0.2 m s ⁻¹ ; at most 0.5 m s ⁻¹
• Home range	Male 500-640 m; female 300-480 m

7.3.2 Introduction

The water vole (*Arvicola terrestris*) is the largest British vole, weighing up to 330 g (Woodroffe 1988). It can be mistaken for a rat but has a rounder body and face, and small protuberant eyes. The fur is usually a shade of brown although partial albinism is common, especially of the tail and forehead. The tail forms 55-70% of its overall length. British voles are slightly larger than their continental conspecifics, with males about 5% larger than females (Corbet and Harris 1991).

The water vole has a wide Palearctic geographical distribution, from Britain to Eastern Siberia. It is absent from Ireland and most offshore islands, though there have been sightings on the Isle of Wight, Anglesey and Arran (Corbet and Harris 1991).

The species was formerly known as *Arvicola amphibius* and subdivided into two subspecies: *A. a. reta* – a smaller, melanic form with a British distribution limited to Scotland; and *A. a. amphibius* – a larger, lighter brown form found throughout Great Britain. There is also a less widely-followed classification of *A. terrestris* into five subspecies (Woodall 1977). Most ecological papers do not specify which subspecies was studied but usually they refer to *A. a. amphibius*.

Kminiak (1967) listed three basic categories of water vole habitat: drainage canals and brooks; permanent waters; and moorlands and peatbogs.

7.3.3 Breeding

Water voles are short-lived, rarely surviving their second winter (Woodroffe 1988). Late-born young of the previous year are less successful breeders than early born young of the same year and individuals are effectively recruited into the breeding population after their first winter (Stoddart 1971).

Non-breeding water voles may nest together in winter, but the social structure of colonies alters with arrival of the breeding season. Females establish defended territories, forming generally monogamous partnerships (though extra-pair copulations by males can occur: Woodroffe 1988). Gender-specific aggression is common amongst water voles, with fierce (sometimes fatal) courtship and territorial disputes among males (Ryder 1962).

After mating, the pair jointly occupy a nest, whilst retaining their old beds. The female gestation period is about 4 weeks and a female may be pregnant and lactating simultaneously (Ryder 1962). The newly-born young are helpless, not leaving the nursery for the first 15 days of their lives; and they are therefore sensitive to flooding of the nursery chamber during this period of time.

Woodroffe (1988) and Woodroffe and Lawton (1990) defined two types of colony: core sites (breeding); and peripheral sites (non-breeding). Latrines (foci for defaecation) are present at core sites but not at peripheral sites; and are normally found on prominent mud banks near

the water's edge. Defecation is a method of both territorial and sexual identification. It is thought that boundary latrines (which are visited most often) serve to discourage neighbouring sexually-mature males from the territory (Woodroffe and Lawton 1990).

Climate appears to be most important in the short breeding life of the water vole, with maximum sexual activity during warm periods (Ryder 1962) and a general occupation of lower-altitude habitats. Woodroffe (1988) cited May as the most important breeding month, with maximum water vole activity in May and June. The breeding season is shorter in Scotland than in Lancashire, probably reflecting lower ambient temperatures (Singleton 1984 and Stoddart 1971: cited by Woodroffe 1988).

7.3.4 Nesting requirements

The nest is usually a complex of tunnels (Corbet and Harris 1991). Having eaten the tender parts of herbaceous plants, the water vole shreds coarser vegetation and uses it to line its nest chambers (Ryder 1962, Corbet and Harris 1991). The water vole is an efficient burrower; but excavation and maintenance of nest chambers are affected by morphology and soil characteristics of the bank; alluvial and light soils are easiest for burrowing (Muller-Bohme 1936).

Bank height and slope

The water vole prefers inhabit banks of a height greater than 1 m whilst banks lower than 0.5 metres are not used (Zedja and Zapletal 1969). The results of their study comparing the numbers of water voles censused at different bank height are shown in Table 7.2.

Table 7.2 The effect of bank height on water vole numbers (Zedja and Zapletal 1969)

Bank height (m)	Catch per 100 m (% frequency)				Sample size
	0-0	0.1-0.9	1.0-1.9	2.0+	
≤ 1.0	62.5	21	12.5	4	24
1.1-2.0	45	25	25	5	20
≥ 2.1	32	23	45	0	22

Higher banks afford more protection from flood events; voles inhabiting an area with higher banks are less likely to have to migrate due to inundation. A certain degree of winter water level rise (during the period of least activity) might actually benefit voles, due to the creation of a 'waterlock' at the entrance to the nest system (Ryder 1962).

Bank angles greater than 35° are best at accommodating water level rises and avoiding flooding (Timson 1991); but the tolerance of many of the water vole's food plant species does not extend beyond 35° (Grime *et al.* 1988). The range of suitable bank slope is therefore a balance between flood avoidance and food availability.

Soil type

Results of a study by Zedja and Zapletal (1969), comparing the numbers of water voles observed in banks of various soil characteristics are shown in Table 7.3.

Table 7.3 The effect of bank soil type on water vole numbers (Zedja and Zapletal 1969)

Bank type	Catch per 100 m (% frequency)				Sample size
	0-0	0-1-0-9	1-0-1-9	2-0+	
Paved or stony	83	17	0	0	12
Paved, with vegetated earth layer	50	25	25	0	4
Sand / loam, unvegetated	56	12	25	7	16
Sand / loam, vegetated	29	29	38	4	34

It was concluded that stony or reinforced banks were unsatisfactory regardless of their vegetation cover, whilst the suitability of loam or sandy banks is modified by vegetation cover (Zedja and Zapletal 1969). Woodall (1977) regarded vegetation cover as a more important factor than soil type for vole habitat suitability.

No significant difference between vole habitation of banks adjacent to arable fields and those adjacent to pasture has been found (Singleton 1984).

7.3.5 Diet

Woodall (1977) described the water vole as a 'generalist herbivore'. Holisova (cited by Pelikan 1974) suggested a typical water vole diet:

- 75% aerial vegetation parts of plants.
- 20% underground parts of plants.
- 4% flowers
- 1% seeds

The importance of dietary components is modified slightly according to the proportion of energy which is actually assimilated. Golley (1968) calculated that 90% of the calorific value of seeds was assimilated, compared with 48%, 80% and 70% for shoots, roots and flowers respectively. Woodall (1977) suggested that the water vole counteracts poor quality of food with an increase in bulk consumed (i.e. they eat large volumes of aerial vegetation parts rather than a lesser volume of seeds and fruits). The major role of aerial vegetation in water vole nutrition probably contributes to its clear preference for banks with abundant vegetation cover (Kratochvil and Grulich 1961, Zedja and Zapletal 1969, Dean and O'Gorman 1976, Corbet and Harris 1991, Timson 1991). During the winter, voles increasingly rely on below-ground rhizomes as food (Holisova 1965).

Both aquatic and terrestrial vegetation is used as food by water voles. The use of terrestrial vegetation is generally limited to those species found within about 1 m of the water's edge (Ryder 1962, Pelikan and Holisova 1969, Stoddart 1970, Woodall 1977). Pelikan (1974) found that *Phragmites communis* formed 32% of the total vole dietary intake and other studies have often recorded its prominence in the diet. Other emergent macrophytes observed in habitat areas include *Juncus effusus*, *Sparganium erectum*, *Glyceria maxima*, *Phalaris arundinacea*, *Typha latifolia* and *T. angustifolia* (Pelikan 1974, Woodall 1977).

Zedja and Zapletal (1969) and Pelikan and Holisova (1969) listed bank vegetation species associated with water vole habitats. Common species were *Bidens tripartita*, *Polygonum persicaria*, *P. amphibium*, *Urtica dioica*, *Rumex aquaticus*, *Bromus inermis*, *Alopecurus pratensis* and *Poa annua*; less common species were, *Veronica beccabunga*, *Cirsium palustre*, *Ranunculus repens*, *Myosoton aquaticum*, *Mentha arvensis* and *Dactylis glomerata*.

Although this listing was drawn from Czechoslovakian studies most of the species are common throughout Britain, exceptions being *Rumex aquaticus* (rare) and *Bromus inermis* (locally naturalised). Most of the other listed species are characteristic of damp, grassy meadows and waterway banks (Singleton 1984).

Woody vegetation is characteristically absent from water vole habitats (Zedja and Zapletal 1969). Shading by tree canopies inhibits many of the grass and ruderal species which comprise the vole's diet. When feeding, the water vole clears a circular 'lawn' of vegetation around the burrow and does not tend to travel very far (Ryder 1962, Dean and O'Gorman 1976). The tender meristems and stems of herbaceous plants are preferred to woody vegetation (Corbet and Harris 1991, Ryder 1962), except perhaps young willows (Glue 1974, Howes 1977). Woody vegetation therefore increases the minimum foraging area to be covered by an individual vole, decreasing efficiency and bringing an added predation risk.

Dean (1947), in his observations of a water vole population, recognised 'eaten' and 'avoided' plants. Avoided plants were *Impatiens* sp., *Filipendula ulmaria* (may be eaten during winter months: Corbet and Harris 1991), *Valeriana* sp., *Myosotis* sp. and *Circaea hitetiana*. Presumably an abundance of one or more of these species would make a habitat less suitable for feeding.

7.3.6 Predation

Predators

Many species have been recorded as vole predators (Ryder 1962, Glue 1974, Howes 1977, Woodroffe 1988). These include birds (heron, kestrel, short-eared owl, tawny owl, barn owl, little owl); mammals (otter, stoat, weasel, fox, cat, pine marten, polecat, mink, brown rat); fish (pike, brown trout, eels); and reptiles (grass snake). The barn owl, especially, feeds almost exclusively on small mammals and is a major predator of water voles, which are amongst its largest prey items. Quantitative estimation of the importance of water voles in predator diets has been difficult, as the fur is indigestible which may bias fecal analysis (Jeffries *et al.* 1989).

Birks (1981) found the remains of water voles in 5% of mink faeces. Adult *A. terrestris* are probably the optimum prey size for mink (Woodroffe *et al.* 1990) and their burrows are too large to exclude the predators (Woodall 1977). There has been a long-term decrease in vole activity at sites where mink are prevalent. Woodroffe (1988) found that 'peripheral' (non-breeding) water vole sites were subject to highest mink activity; suggesting that predation by mink is a factor in vole habitat selection (Jeffries *et al.* 1989). Mink and water voles presently coexist; but there is a growing concern that the spread of mink might lead to local extinction of water voles (Lever 1978a, 1978b, Linn and Chanin 1978a, Woodroffe 1988).

Refuges

In areas with extensive vegetation cover, each vole constructs a series of 'runways' (4-9 cm wide) within 1 m of the water's edge. These runways are memorised according to direction ('kinesthetically': Corbet and Harris 1991) and provide escape routes from predators. The agility of the water vole on land is equivocal: it has been described as 'clumsy' (Stoddart 1977) and as 'racing up and down the river bank' (Woodroffe 1988).

The basic anti-predator behaviour of the British water vole is to swim. Woodall (1977) remarked on the greater reliance of the water vole in Britain on escape to water than its

continental conspecifics. This is probably due to its larger size and therefore burrow diameter, which means that predators can continue to pursue the vole if it does not lose them before reaching its nest. The noisy entry of the vole into the water may act as a warning of the predator threat to other voles in the vicinity (Ryder 1962). The water vole can only stay submerged for a period of about 20 seconds (Ryder 1962) since its blood is not specialised for diving, unlike some other aquatic mammals (Corbet and Harris 1991). Part of the success of mink as predators of the water vole arises because they can maintain pursuit into the water.

Many water voles have an underwater entrance to their nest system: they scabble at the bottom of the stream to increase the turbidity of the water, preventing predators from locating the entrance of the burrow (Woodall 1977). Hence the vole is most likely to escape predation in streams with silty bottoms, or where the water is already turbid. Water voles have been observed to prefer streams with silty bottoms (Ryder 1962, Zedja and Zapletal 1969, Woodall 1977). Zjedja and Zapletal (1969) produced a table which summarises a study on the effect of stream bottom characteristics on observed numbers of water voles (Table 7.4).

Table 7.4 The effect of stream bottom on water vole numbers (Zedja and Zapletal 1969)

Substratum	Catch per 100 m (% frequency)				Sample size
	0-0	0-1-0-9	1-0-1-9	2-0+	
Pavement or stones	92	8	0	0	13
Pavement, covered with silt	25	50	25	0	4
Sand	90	0	0	10	10
Silt	23	31	44	2	39

Undermined banks are preferred because they hide the lower aerial and submerged entrances to nesting systems (Zedja and Zapletal 1969). Prime sites, however, are not actively eroding and are vegetated to the edge of the water.

Woodall (1977) stated that water voles prefer deep streams, to be more quickly out of reach of most predators in an escape. The water vole also exhibits a preference for streams at least 1-3 m wide, though the reasons are unclear (Harrison-Matthews 1963).

Zjedja and Zapletal (1969) found preference for stream velocity less than 0.5 m s⁻¹ (mostly below 0.2 m s⁻¹); and Pelikan and Holisova (1969) found no relation of movement direction and flow direction at 0.2-0.3 m s⁻¹. The erosive force of higher-velocity streams might lead to frequent bank subsidence, compromising vole colonies and their vegetation diet.

7.3.7 Competition

Lawton and Woodroffe (1991) proposed that, along with predation, interspecific competition is a major factor affecting the water vole's range.

Zjedja and Zapletal (1969) caught several other small mammals in a study of water voles. These were water shrew, pygmy shrew, wood mouse, brown rat, Orkney/Guernsey vole and muskrat. Of these, at least one (the muskrat) is known to be a competitor for space with the water vole (Kratochvil and Grulich 1961), and as such might limit resource availability.

Intraspecific competition may also lead to the habitation of sub-optimal 'peripheral' sites by subordinate water voles (Woodroffe 1988). These sites are non-breeding colonies, and are

only used for temporary habitation until a more suitable residential site is available (for example a non-breeding female often takes over the territory of her mother). Home range lengths of individual water voles are not large (maximum reported ranges are 500 m and 300 m (Corbet and Harris 1991) or 640 m and 480 m (Pelikan and Holisova 1969) for males and females respectively).

7.3.8 Human activities

A negative influence of human activity on water vole habitation has been recorded (Kratochvil and Grulich 1961). Dredging is often cited as the most frequent habitat disturbance for water vole populations (Jeffries *et al.* 1989). However, mowing appears to be equally detrimental to the water vole carrying capacity of a river bank. Mowing reduces vegetation cover and therefore increases predation risk (Kraft 1960). Singleton (1984) found that mowing and dredging significantly reduced the water vole population, especially affecting adult males. Singleton suggested that this was due to adult males being more active than females at the times of mowing (July), when reproductive females would be spending most of their time suckling young in the nest. Stomach analysis has also shown that the diet of water voles alters after mowing has taken place, with a decrease in aerial vegetation plant parts and a change in species composition (Holisova 1965). Mowing may displace voles away from their permanent sites to sub-optimal, temporary sites (Zejda and Zapletal 1969).

The water vole is diurnal and so is disturbed by anglers, walkers and other amenity users (Jeffries *et al.* 1989).

Pollution was suggested by Jeffries *et al.* (1989) as a possible cause of decreasing water vole numbers in Britain, although Howes (1977) described the water vole as 'a familiar sight on the grossly polluted rivers and canals of south and west Yorkshire'.

7.4 Water shrew (*Neomys fodiens*)

7.4.1 Habitat summary

- | | |
|----------------------|--|
| • Distribution | See map (Figure 7.4), recently rocky shores in Scotland. |
| • Water chemistry | Sensitive to pollution. |
| • Water clarity | Clear. |
| • Aquatic vegetation | Watercress beds. |
| • Substratum | Silt |
| • Home range | Reported as 106-207 m ² ; and 20-30 m ² (land), 60-80 m ² (including water) |

7.4.2 Introduction

The water shrew (*Neomys fodiens*) has proved difficult to study due to the small, localised nature of British populations (see Figure 7.4). It usually colonises sites adjacent to clear, unpolluted streams and ponds wherever there is adequate cover – especially in the presence of watercress beds. In northwest Scotland, distribution may extend to the boulders of rocky beaches. Water shrews are semi-aquatic, and burrow into riverside banks forming extensive, shallow tunnel systems, with entrances of approximately 2 cm diameter either above or below the water surface (Corbet and Harris 1991).

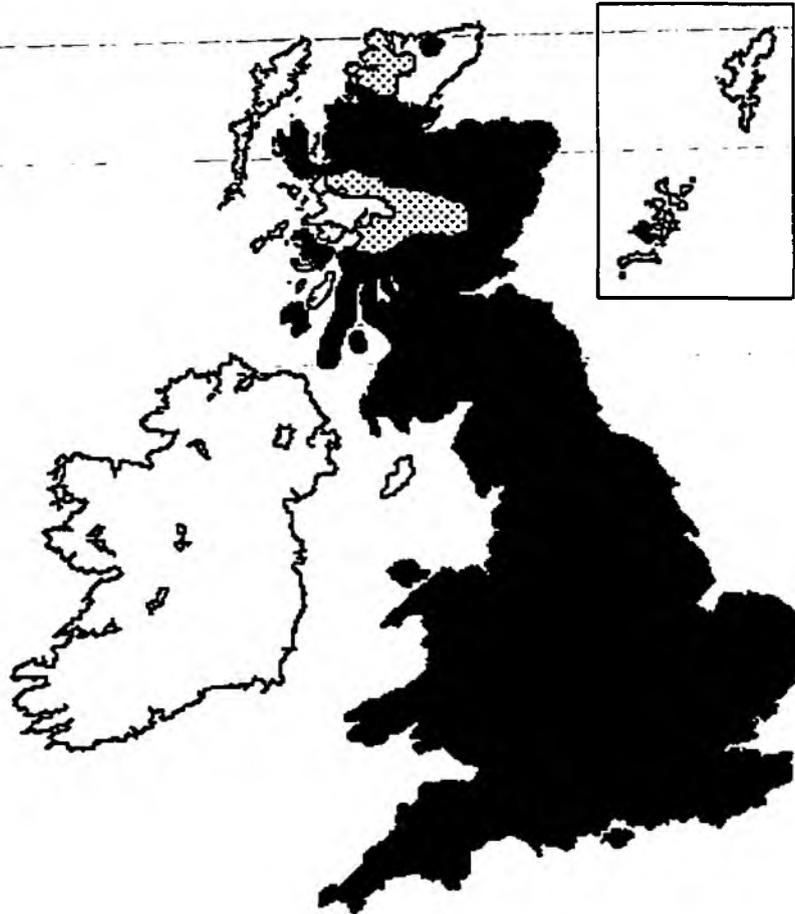


Figure 7.4 Distribution of the water shrew in the British Isles (Corbet and Harris 1991)

7.4.3 Breeding

The breeding season of the water shrew is April-September, peaking in May-June. Most individuals breed in their second year, although some females may do so in their first year (Corbet and Harris 1991). The lifespan of the watershrew is 14-19 months, with mortality highest during autumn and winter. The main predators are carnivorous mammals, owls and fish.

7.4.4 Diet

The activity of shrews tends to be patchy within their territory, and there is rapid movement between focal points. Foraging dives last for a maximum of 4 seconds, which allow diving to 75 cm or more (Churchfield 1985). Due to these physiological constraints on dive duration, the shrew selects convenient access points to the river, such as water-level berms (Lardet 1988).

This shrew has a wide-ranging diet of invertebrates (e.g. Diptera larvae) and vertebrates (e.g. fish and frogs) but aquatic invertebrates are generally prevalent (Churchfield 1985). Wolk (1976) found a seasonal difference in the relative importance of different items, though all of the food items were aquatic species (Table 7.5).

Table 7.5 Composition of the autumn and winter diet of the water shrew (Wolk 1976)

Dietary item	% of food remains		Dietary item	% of food remains	
	Autumn	Winter		Autumn	Winter
Mollusca			Insecta		
<i>Anisus</i> sp.		0.1	<i>Anabolia</i> sp.		0.4
<i>Anodonta</i> sp.		0.6	<i>Limnephilus</i> sp.		38.0
<i>Bathyomphalus contortus</i>		0.1	<i>Molanna</i> sp.	3.3	1.1
<i>Bithynia tentaculata</i>		1.5	<i>Notidobia</i> sp.	0.7	6.5
<i>Galba corvus</i>	1.3	4.1	Trichoptera indet.		2.5
<i>Galba truncatula</i>		0.1	<i>Dytiscus</i> sp.	0.7	0.9
<i>Lymnaea stagnalis</i>		0.3	<i>Nepa</i> sp.	8.6	6.0
<i>Pisidium</i> sp.		0.3	Amphibia		
<i>Planorbarius corneus</i>	4.0	1.3	<i>Rana temporaria</i>	14.6	20.2
<i>Planorbis planorbis</i>	0.7	0.1	<i>Bufo bufo</i>		0.1
<i>Radix peregra</i>	58.3	1.1	Pisces		
<i>Segmentina nitida</i>	0.7	0.1	<i>Gasterosteus aculeatus</i>		2.0
<i>Viviparus contactus</i>	1.2	0.6	Mammalia		
			<i>Sorex araneus</i>		0.1

A study of water shrew faeces (in watercress beds of southern England) recorded a dietary size range from <4 mm (Acari, Ostracoda, larvae of Chironomidae and Simuliidae) to >40 mm (larvae of Tipulidae and larger Trichoptera), though the smallest sizes might involve accidental ingestion (Churchfield 1984, 1985). Churchfield found that 33-67% of the total diet was of aquatic origin: predominantly *Asellus*, *Gammarus*, Trichoptera larvae and Diptera larvae. Buchalczyk and Pucek (1963) observed caches of food such as snails and frogs. They may have been food stores *per se*, or simply be consumption sites holding a temporary surplus of captured items. The water shrew is active for about 12 hours per day throughout the year (Lardet 1988) – the high metabolic rate of these mammals probably prevents winter inactivity (e.g. hibernation) – one shrew weighing 15.6 g had a daily ration of 18 g (Tupikova 1949: cited by Corbet and Southern 1977). Some laboratory-based studies have suggested that winter inactivity does occur, but this is in an artificial environment of constant, surplus food supply.

7.4.5 Home range

The home ranges of water shrews may overlap, despite their solitary nature (Corbet and Southern 1977). Estimates of the home range size of the water shrew vary: Lardet (1988) cited a range of 106-207 m²; whilst in West Germany figures of 20-30 m² of land (60-80 m² including water) have been found (Iling 1981). The home range increases for both sexes during the reproductive season.

7.5 Mink (*Mustela vison*)

7.5.1 Habitat summary

- Distribution See map (Figure 7.5)
- Flow Slow.
- Channel dimensions Shallow, narrow rivers and streams.
- Terrestrial vegetation Abundant – especially *Phragmites*.

• Tree species	Oak, sycamore, willow, birch.
• Nutrient status	Eutrophic.
• Den sites	Eroded root systems, bridge structures, rabbit burrows.
• Den spacing	200-500 m
• Dens per territory	Six (range 2-10)
• Territory length	Usually 1.5-3 km; up to 5 km in poor habitat.



Figure 7.5 Distribution of mink in the British Isles (Corbet and Harris 1991)

7.5.2 Introduction

The mink is a mustelid (closely related to ferret, stoat, weasel and pine marten) introduced widely to Europe. Its diet consists mainly of fish, birds and smaller mammals such as rabbits and water voles. The body is elongate with a tail that represents 30% of the overall length (Birks 1986). The legs are relatively short and despite its aquatic habit, the feet only show limited webbing between the toes. Its size is very similar to that of the ferret: an average male adult mink weighs approximately 950 g; and an adult female about 600 g (Swan 1982). The colour of mink can vary from white to browns, greys and black (Swan 1982). After a few generations in the wild, it reverts back to a dark brown colour with patches of white on the chin and chest (similar to the indigenous race of North America).

Mink mate in the spring with each female giving birth to 3-5 young in late April or early May. When juveniles reach approximately 3 months, they leave their mothers and become vagrant, passing through existing territories until a suitable habitat for settlement is found. Each adult mink occupies its own territory within which it hunts; the boundaries are demarcated by deposition of urine and faeces. Male and female territories sometimes overlap during high population density, but mink of the same sex have never been found to coexist. The territory is usually 1.5-3 km of river (Birks 1989), varying with food availability.

7.5.3 Origins

The mink is not a native of the British Isles. The species commonly found here is the North American mink (*Mustela vison*) which has a history of trapping and captive breeding for its fur. The first American mink were brought to British 'fur farms' in 1929 (Usher 1986). Regulations governing fur farms were initially lax and escapes of individuals into the wild were common. Successful breeding of feral mink were not recognised until 1956 and survival rates were grossly underestimated: it is now known that a captive mink can start to hunt successfully within just a few hours of escape (Alexander 1984).

By 1962, approximately 700 fur farms existed in the UK and widespread releases had occurred (Usher 1986), serving as centres for their initial patchy colonisation. All farms were eventually brought under legislative control by the Mink (Importation and Keeping) Order, made under the 1932 Destructive Imported Animals Act. In the 1960s, MAFF trapped over 5000 mink in England and Wales. Subsequently, few escapes occurred but the spread of feral mink continued by expansion of existing populations. Relatively few mink are now reared in Britain: in 1981 the total production was 245 000 pelts from only 67 farms (Dunstone 1986).

The mink is now common and widespread in the British Isles, although there are still some areas where it is patchy or absent (see Figure 7.5). These include northwest Wales, Scotland north of the Great Glen, and parts of East Anglia. In England, colonisation is generally more complete in the south.

The spread of mink has been rapid due to its colonisation of a wide range of aquatic habitats. In Scotland, the speed of range increase is approximately 20 km per annum; a similar rate in Iceland has resulted in dispersal throughout the island in just 35 years (Smal 1988). Colonisation of coastal islands has also occurred as a consequence of the mink's strong swimming ability. Most movement occurs when juvenile mink are in search of new habitats suitable for colonisation. One male has been recorded moving 20 km in just six days but territorial migration of about 12 km is more usual (e.g. along the River Teign: Usher 1986, Birks 1989).

Mink in Britain occur on every kind of waterway including upland streams and broad lowland rivers and canals, with records from ponds, lakes and reservoirs, estuaries and rocky coastlines. The preferred habitat in fresh water is slow flowing streams and small rivers, with a high nutrient content and an abundance of cover next to the water's edge (Birks 1986). Although mink are closely associated with waterside habitats, they are capable of living for long periods away from waterways, provided that prey such as small mammals and birds are available. Mink are often found away from water at times when the associated food availability is seasonally depressed; or when the population pressure is high; or during the mating season.

7.5.4 Diet

Mink are often described as generalist predators because of flexibility in their hunting behaviour. Birks (1986) described them as a 'jack of all trades' - hunting prey on the ground,

in burrows, underwater and occasionally in trees. Mammals, birds, fish, amphibians and invertebrates all feature in the diet of mink. Variation has been shown in the importance of prey species (Table 7.6), mainly related to their availability in terms of abundance, seasonality and ease of capture (Thompson 1971, Dunstone and Birks 1987).

Table 7.6 Summary of several mink dietary analyses (various sources)

Site	Fish	Birds	Mammals	Source
Scotland				Cuthbert (1979)
R. Tweed	72%	5%	13%	
R. Urr	60%	5%	20%	
R. Sheeoch	57%	15%	17%	
Total	67% (31% salmonids, 23% eels)			
Scotland	49% (salmonids dominant, eels absent)	28% (of which 29% mallard, 25% passerines, 13% coot/moorhen)	23%	Akande (1972)
Britain	54%	11%	29%	Dunstone and Birks (1985)
Britain				Linn and Chanin (1978a)
R. Frome	33%	-	-	
R. Teign	50% (of which 70% salmonids, 30% eels and loach)			
Slapton Ley	50% (of which 50% eels, 50% perch, sticklebacks, and cyprinids)	33%		
England and Wales	Coarse fish (no salmonids)	33% (of which 50% waterside species)	33%	Day and Linn (1972)

In some cases, predation of ground nesting birds and their eggs has occurred (Angelstam 1986) but the dietary contribution of eggs is less than 1%. Some woodland and game birds are also taken in small numbers. A wide range of fish species are eaten by the mink: slower-swimming coarse fish are selected if available, with a general preference for eels. Mink can swim well underwater but rarely stay submerged for more than 10 seconds, so shallow water is preferred. Most fish taken are less than 15 cm long (eels up to 30 cm). Amphibians such as *Rana* are taken occasionally, as are some invertebrates such as crayfish and earthworms.

Eberhardt and Sargeant (1975) found that the availability and location of suitable rearing dens on prairie marshes in America influenced the distribution of foraging. Gerell (1970) also found that female mink impacted areas near to their den sites most intensely.

7.5.5 Dens

Den availability is very important in habitat choice, since mink spend most of their time sleeping or resting. Birks (1986) found that 84% of the time of mink on the Galloway coast was spent in dens; sleeping, grooming or eating food. Mink rarely dig their own dens and prefer to use ready-made holes: rabbit burrows are often used, usually after the original owner

has been eaten. An analysis of dens used in Devon revealed that water-side trees were the most popular sites, especially oak and sycamore with cavernous and eroded root systems (Birks 1986). Mink can use a variety of den sites when they are in short supply, such as among block-stone bridge foundations on channelised rivers.

Mink maintain marked territories with a number of dens in regular use, except for breeding females which use a single den in May-June. Birks (1986) found the number of dens in use by mink was 2-10 (mean 6) in Devon; found that the average. Most home ranges of mink studied by Linn and Stevenson (1980) contained 6-10 dens, spaced at intervals of 200-500 m. The number of dens is dependent on territory length: Birks (1986) proposed that this reflects the awkward shape of a long thin territory which cannot be easily defended or exploited from a single central den. The most important (regularly-visited) boundaries are at the upstream and downstream ends, but mink need refuge available throughout while foraging. Foraging areas are used on a loose rotational basis but sites can be favoured seasonally due to prey abundance, such as a rabbit hedgerow or concentration of eels. Dens are used to store food, and as a refuge for its consumption. Mink accumulate large caches of food in their native habitats where they are subject to severe climatic conditions.

Schladweiler and Storm (1969) found that the tunnels were typically 10-15 cm diameter, situated at the boundary of sedge mat and upland; within 200 yards of open water. The mink did not use the same dens repeatedly, but tended to use the most convenient dens available. Birks and Linn (1982) found the mean number of dens used in November-April was 4 compared with 8.8 in May-October. The majority of stays were less than one day, but this increased in winter months. They suggested that the dependence on existing burrows, together with a tendency to concentrate foraging activities close to den sites, means the presence of potential den sites is a very important factor of habitat requirement for mink. Where potential den sites are abundant (for instance rocky, tree-lined stretches) the selection of dens may be secondarily determined by other factors such as prey distribution. However, where the nature of the habitat is such that den sites are limited and prey is uniformly abundant (as in marshy areas), the distribution of den sites may dictate the distribution of foraging activity and other home range characteristics.

Dens found by Gerell (1970) were most commonly located in cavities under tree roots in river banks, generally with one or two entrances above the water surface. Other den sites were those provided by piles of stones, often in bridge abutments - these were generally preferred as they were well above the water surface, and therefore less affected by the changes in water level. Dunstone and Birks (1985) compared coastal, riverine and lacustrine habitats and found them to have to have a decreasing range of potential den sites. Within the riverine habitat, 42% of dens occurred in or beneath trees; and many were burrows vacated by other animals.

7.5.6 Vegetation cover

Corbet and Harris (1991) suggested that mink favour eutrophic streams and rivers with abundant bankside cover and eutrophic lakes fringed with reeds. They are less abundant where waterside cover is sparse or absent, because reedbeds provide good places to hunt waterfowl and fish. Denning facilities and cover are important (Mitchell 1961, Cuthbert 1967, Gerell 1967); the amount of cover influences home range size and population density. Seashore and peaty moorland environments are therefore less suitable for mink than rivers, even in arable areas. Birks and Linn (1982) found that waterside trees were important as potential den sites on the River Teign, River Exe and Slapton Ley. At all three sites, it was found that oak, willow and sycamore were most used. Gerell (1970) similarly found willow and birch trees to be significant, in addition to a high density of *Phragmites*.

7.5.7 Home range

The home range of the mink tends to hold restricted areas of intense use known as 'core areas' (Gerrell 1970). Home range size is influenced by population pressure as a function of population density in relation to the carrying capacity, which for mink is determined by food, cover and den-site availability (Birks 1986). Poor habitats for mink are therefore those waters where bankside cover is thin or absent; or where prey are scarce, as in many acid upland streams. In poor habitats, mink may hold territories up to 5 km of river. Where food is very scarce the length of river mink would need to defend in order to feed themselves may be too great, so they adopt a drifting or 'transient' lifestyle until they find a more suitable vacant stretch. In the best habitats, with abundant food and cover, mink may occupy territories as short as 1 km. Quantitative evidence of the relation between territory and habitat productivity was provided by Dunstone and Birks (1985) and Corbet and Harris (1991).

Home ranges are larger where the social environment is unstable, due to the absence (or frequent removal) of neighbours. Dunstone and Birks (1985) found the territorial system to be most unstable on the River Teign due to the tendency of mink to vacate their territories after only a few months. Territories also tended to be larger and less compact. They concluded that stability and density of home ranges varied according to environmental suitability, in terms of important habitat features.

7.5.8 Activity patterns

Birks and Linn (1982), found that movements between dens were made along linear habitat features such as river banks, lake margins, feeder streams and hedgerows – all characterised by vegetative cover. The extent, pattern and frequency of inter-den movements varies between individuals; and males typically move 1000 m compared to 534 m for females.

Dunstone and Birks (1985), found that male and female activity patterns differed seasonally. Male foraging behaviour was most apparent during late summer and autumn; whilst females showed a peak of inter-den activity during April-May, the late gestation and lactation period. In all three sites that they studied (riverine, lacustrine and coastal), most activity was nocturnal (also Thompson 1971), with only 5-20% of each 24 hours spent in foraging and travelling between dens. Corbet and Harris (1991) reported that movements within the home range include patrolling, with regular visits to the boundaries. They found that in all cases, activity patterns are subject to modification by the predominating diet. Mink on the coast may follow a tidal cycle; whilst rabbit predation can lead to a very unpredictable pattern, as they can provide sufficient food for several days.

Movements outside core areas serve not only as territory patrol but also for monitoring prey availability in the remainder of the home range (Thompson 1971). Such behaviour would allow a resident mink to respond rapidly to relative changes in prey availability by shifting its foraging patterns accordingly.

7.5.9 Mortality

A great number are trapped and killed by farmers and gamekeepers; and some are hunted and killed by packs of mink-hounds in the summer months. Apart from man, feral mink have no significant predators in the British Isles and very little is known about the natural causes of death. Large raptors such as golden eagles and hen harriers may take them occasionally, and there are reports of predation by badgers (Birks 1986). It seems that for the most part, mink numbers are regulated by their own territorial behaviour rather than predation; and many of those which fail to establish a territory probably die of starvation and disease.

7.5.10 Competition

The mink's flexibility in hunting means that it usually needs only to hunt prey that are abundant; and therefore is unlikely to eliminate a prey species. Mink have often been accused of impacting the otter, although the latter is a bigger animal and a superior fisherman. A large amount of research has been carried out on the extent to which the mink and otter compete for food and habitat, and significant dietary separation has been noted between these two species in the Irish Midlands (Kyne *et al.* 1989). Mink were found to consume more birds and mammals, and fewer fish than the otter, which is more adapted to hunting in water (Poole and Dunstone 1976). Otters also tend to prefer larger prey items than mink – with 30% of fish taken by the otter exceeding the maximum size of fish taken by mink (Erlinge 1969) – and therefore the two species occupy slightly different niches. Favoured habitat features also differ: mink prefer mature willow trees, saplings and shrubs with dense cover; whilst the otter frequents areas holding mature sycamore and ash (Stoddart 1983). There is some evidence to indicate that mink and otter compete for food under geographical/seasonal shortages of their food resource (Akande 1972), but the rarity of any obvious competition between feral mink and native carnivores would seem to suggest that it has filled a previously unoccupied ecological niche.

7.5.11 Effects of mink as predators

It has been alleged that mink have detrimental effects on farming stock, wildfowl reserves and commercially important fishing sites; and that they deplete small mammal populations and threaten important bird species, especially in coastal regions. Alternatively, mink may not be a novel threat to wildlife, different from indigenous mustelids such as the weasel, stoat, polecat or otter (Linn and Chanin 1978a). Prey species have developed ways of mitigating predation by indigenous mustelids but the polecat and otter have both been reduced by man's activities, so mink must have at least a quantitative effect on predation pressure.

The impact of mink on game and wildfowl is the greatest where densities of these species are high, such as pens of hand-reared fowl. Domestic poultry and Wildfowl Trust / RSPB reserves have suffered many mink attacks (Lever 1978). Surplus killing rarely occurs in the natural environment (e.g. grebes in British Columbia: Breault and Cheng 1988) but may happen in enclosed places, either with the 'normal' intent of storage or through disorientation.

Arnold and Fritzell (1987) studied mink scats in Manitoba prairie wetlands, where their normal foods of fish and crayfish were limited. Although use of avian prey rose sharply in the breeding season, the impact was not sufficient to account for a decline of waterfowl. A decrease in the numbers of wildfowl in Ireland (especially mallard, tufted duck and moorhen) has coincided with the expansion of the mink population to affected areas (Smal 1988), but no direct evidence linking these events has been published.

Introduction of mink to small islands can be disastrous for resident birds, especially where there are large colonies of ground nesting birds and no native ground predators (Lever 1978, Linn and Chanin 1978b, Smal 1988). Planning permission to build a mink farm on the island of Westray (in the Orkneys) was originally granted (Glue 1978) until the extent of the damage that could be caused to the bird populations by escaped mink became clear.

Predation of mink on fish such as salmon and trout has been variously described as advantageous (Linn and Chanin 1978a), having no effect (Chanin and Linn 1980), and detrimental (Heggnes and Börgstrom 1988). Advantageous effects on fish stock quality could be brought about by the removal of smaller individuals leaving more available food for each fish, thereby producing bigger specimens for angling (Linn and Chanin 1978a). Comparative fishing catches along the River Teign showed no evidence of population depletion in fisheries subsequent to mink colonisation (Chanin and Linn 1980). Conversely, a case study in Norway

indicated that a high mortality of brown trout and Atlantic salmon coincided with occupation by mink (Heggnes and Børgström 1988). In this case, salmonids were the only prey species present. It appears that salmon are not selectively hunted by mink; their predation will often be mitigated by the presence of alternative prey items.

Rabbits, mice and rats are all eaten by mink; but this predation does not generally appear to restrict their populations. Along the River Teign (Devon) mink numbers doubled between 1972/4 and 1978/80; but the local rabbit population displayed a concomitant increase (Birks 1989). Woodroffe *et al.* (1990) suggested that the water vole could be susceptible to mink predation. The adult voles are close to the optimum prey size for adult mink; not agile enough to escape predation on land or water; and their burrows are not small enough to exclude the mink. Their usual escape mechanism of diving into the water is rendered ineffective against the mink, which has proven to be a competent predator in aquatic environments.

7.5.12 Population control

Natural predators of the mink are scarce. In central and western Europe, mustelids have been found to feature in the diet of 17 different birds (Korpimäki and Norrdahl 1989), although they only constitute a very small proportion of each birds' diet. Otters and foxes have only rarely been known to kill mink (Smal 1991). Artificial measures for the control of mink populations have met with little success. Most trapping procedures are only effective at removing transient mink – individuals that are likely to disappear from an area anyway. If resident mink are trapped, then their territories are quickly recolonised. In such cases, removal of a territory-holding mink could actually result in a temporary increase in the mink population of an area whilst young mink compete for the vacant territory (Smal 1991). Hunting has also proved to be an ineffective control measure (Birks 1989). In some areas of Norway, feral mink numbers decreased during the past 10 years (Bevanger and Albu 1986). The freshwater fish in these areas, which formed an important dietary component, are now virtually extinct due to acidification.

Populations of mink are essentially self-regulating and stabilise at the carrying capacity of the environment (Smal 1988). Stress, weight loss and mortality occur in the winter and spring due to the limitation of food supplies and the onset of the mating season (Smal 1991).

7.6 Bats

7.6.1 Habitat summary

Daubenton's bat (*Myotis daubentoni*)

- | | |
|-----------------------|---|
| • Distribution | See map (Figure 7.6) |
| • Channel width | Wide, over 9 m |
| • Velocity | Slow, pools (calm water) |
| • Bankside vegetation | Deciduous woodland. |
| • Roost sites | Within 200 m of water: tunnels, tree holes, bridges, caves. |
| • Roost spacing | 236-800 m |
| • Foraging area | At least 0.5 ha |



... and all areas south

Figure 7.6 Distribution of Daubenton's bat in the British Isles (Corbet and Harris 1991)

Natterer's Bat (*Myotis nattereri*)

- Distribution See map (Figure 7.7)
- Channel width Wide.
- Flow No preference.
- Bankside vegetation Diverse.
- Roost sites Buildings, mines, quarries, coniferous trees.



... and all areas south

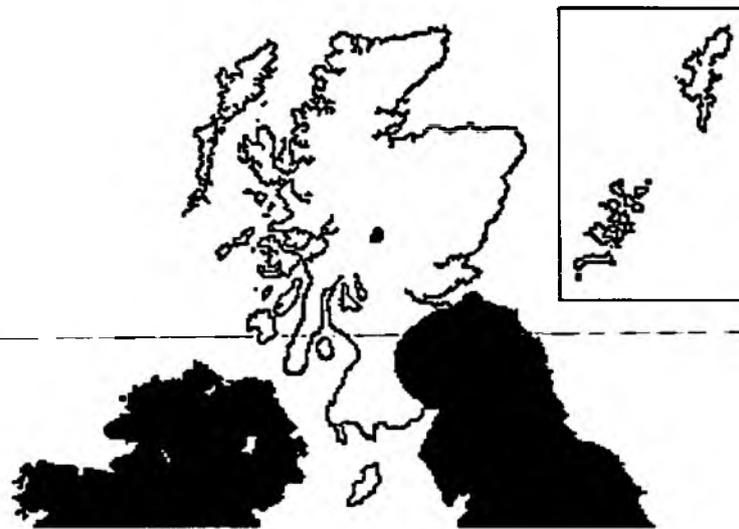
Figure 7.7 Distribution of Natterer's bat in the British Isles (Corbet and Harris 1991)

Pipistrelle (*Pipistrellus pipistrellus*)

- Distribution Throughout British Isles, except Shetland.
- Channel width Wide (over 9 m)
- Flow No preference.
- Bankside vegetation No preference.
- Roost sites Buildings, domestic attics etc.

Whiskered Bat (*Myotis mystacinus*)

- Distribution See map (Figure 7.8)
- Channel width Narrow, less than 9 m
- Flow No preference.
- Bankside vegetation Abundant, trees and shrubs 1-5 m height.
- Roost sites Trees, buildings and caves.



... and all areas south, except Isle of Wight

Figure 7.8 Distribution of whiskered bat in the British Isles (Corbet and Harris 1991)

7.6.2 Introduction

There are fifteen species of bat resident in Great Britain – all of which are subject to legal protection. All species are insectivorous; but each uses different habitats and strategies for hunting prey and rivers provide good hunting grounds for some. The species most frequently foraging in the riparian zone is Daubenton's bat (also called the water bat). The whiskered bat occurs in both wooded and open countryside and is often associated with water. Most work on feeding ecology has studied the pipistrelle: this species often roosts in buildings and can be easily caught, sampled and marked. Its foraging habitat includes farmland, open woodland, suburban gardens, marshes and urban centres; but it has been recorded feeding on the rich insect fauna around rivers, particularly in the Grampian region of Scotland (Racey *et al.* 1985).

Natterer's bat is also associated with rivers (Corbet and Harris 1991). It seems to take insects from around bankside plants, though its feeding is less well-studied than that of the pipistrelle. All four species have a wide distribution within the British Isles and the pipistrelle is particularly common.

7.6.3 Roosting and seasonal movements

In Britain, bats colonise natural structures such as tree cavities, caves and rock crevices. Man-made structures are also exploited as substitutes for natural roosts. Mature trees with holes formed due to age and disease are important roosting sites. Bats can make use of quite small crevices leading to dry hollows - a crack of 1.5 cm width can be sufficient (Lewis and Williams 1984). In the course of a year an individual bat can occupy many roosts, which may be in the same cave or building but are more usually several kilometres apart. Roosts provide sites for mating, hibernation and rearing young; they promote social interaction and the digestion of food; and they offer protection from adverse weather and predators. There are three types of roost: hibernacula, nursery and mating sites.

All species of bat in Britain hibernate in response to depressed food availability between September and May. The hibernation site must provide security from predators, as well as a suitable physical environment. In winter, caves are mainly used for hibernacula as they provide the most effective protection against extremes of temperature. Bats are the only group of British vertebrates to successfully exploit caves for permanent shelter and have virtually no roost competitors. Caves are however, the least abundant roost type - a significant disadvantage for Daubenton's and Natterer's bats, which rely most on them for winter hibernacula. The provision of artificial caves might be a viable way of increasing bat populations (Mayle 1990). Suitable tree holes could be saved by steering forest practices away from the felling of larger, dead trees (Ratcliffe and Petty 1986); alternatively, bat boxes could be more widely introduced.

In the spring, the sexes separate and the females move to regularly-used summer roost sites. Bats usually hibernate singly or in small groups but the summer roost has to be large enough to accommodate several hundred nursing females. (Humphrey 1975) proposed that the availability and quality of nursery roosts is an important control of Nearctic bats; and this may also be true for those in Britain.

The suitability of a foraging habitat may be influenced by nearby roost availability and location (Kunz 1982). No species in Britain is known to migrate very long distances between roost sites: for Daubenton's and Natterer's bats, the longest recorded movements in Britain are 19 km and 24 km respectively.

Daubenton's roosts are found in close proximity to water in tree-holes, under bridges, in tunnels, in buildings and caves (Mayle 1990). The distances travelled between roosts and foraging area in Denmark averaged 236 metres with a maximum of 800 metres (Nyholm 1965) and all nursery roosts in Finland were within 200 metres of water. Along the River Spey in Scotland, Swift and Racey (1983) observed Daubenton's bats approximately 900 metres upstream and 1200 metres downstream of the roost.

Natterer's bats show a preference for buildings (Kunz 1982) though studies on their choice of roost site may be biased towards the more conspicuous roosts in man-made structures (e.g. buildings, disused mines, stone quarries). They occurred mainly in well-wooded coniferous areas of river valleys and lochsides in Scotland (Bullock 1986).

Pipistrelles most often roost in human habitations ranging from churches to modern buildings; they rarely colonise trees or caves (Corbet and Harris 1991). The distances travelled are up to 5 km from the nursery roost (Swift *et al.* 1985).

Whiskered bats roost in trees and buildings during the summer months, possibly overwintering in caves but favouring trees and buildings (Corbet and Harris 1991). Bat boxes may be exploited by this species.

7.6.4 Foraging and diet

Bats use high frequency echo-location while foraging; the short wavelengths providing a good degree of resolution for small objects such as insects. Bats' feeding is important in understanding their habitat requirements in the riparian zone. Foraging strategies fall into three categories:

- Aerial feeding – catching insects mid-flight.
- Foliage gleaning – collecting insects from the surfaces of local vegetation.
- Ground feeding – foraging at ground-level.

Bats may utilize one or a combination of these strategies depending upon flight capability, echo-location and the availability of flying insects. Almost continuous feeding is necessary because of heat loss (high surface area / volume ratio) and the energetic cost of flying: a bat may thus consume 25% of its body weight in a feeding session.

Several factors within the riparian habitat affect insect availability – most obviously the variety and abundance of plants and trees. Vegetation provides both substrate and shelter for insects, and Mayle (1990) cited several studies inversely relating aerial insect abundance with exposure and wind speed.

The relative abundance of bats in Scottish river valleys was related by Racey and Swift (1985) to the quantity of insect larvae in the rivers, with most in clean rivers free from pesticide runoff. Insect density is greater over pools than riffles at a height of c. 2 m above water level (Frenckell and Barclay 1987: cited by Mayle 1990) and this abundance of prey might explain the increased foraging activity of certain bat species over calm pools (Sargent-1991).

Daubenton's bat

Daubenton's bats forage over (or close to) water and riparian vegetation, with a preference for wooded habitats (Jones and Rayner 1988, Sargent 1991). Activity is greatest 1-4 hours after sunset. Swift and Racey (1983) observed Daubenton's bats feeding along the River Spey (and nearby lochs) where they foraged in long straight beats, less than 1 m above the water. There is no difference in insect abundance over pools versus riffles at such heights (cf 2 m) but turbulent water may distort the process of echo-location to make foraging less successful, and this may be an additional benefit of hunting over pools (Sargent 1991).

The diet of Daubenton's bat was investigated by examination of faecal pellets collected from below roosts (Swift and Racey 1983: see Figure 7.9). Nematocera and Trichoptera contributed most to the diet, whilst other prey items included Neuroptera, Coleoptera and Lepidoptera. Ephemeroptera were also taken when available but no flightless insects were eaten. Relative proportions of prey items identified within faecal pellets were very similar to the proportions of each insect species found in trap samples from the foraging habitat.

Another faecal analysis found fragments of chironomid larvae and parasites associated with freshwater gastropods. Jones and Rayner (1988) called this feeding strategy 'gaffing', whereby prey is taken from the surface with the feet or possibly the interfemoral membrane (the membrane around the tail). Observations of gaffing are, however, rare, and aerial feeding is the predominant strategy.

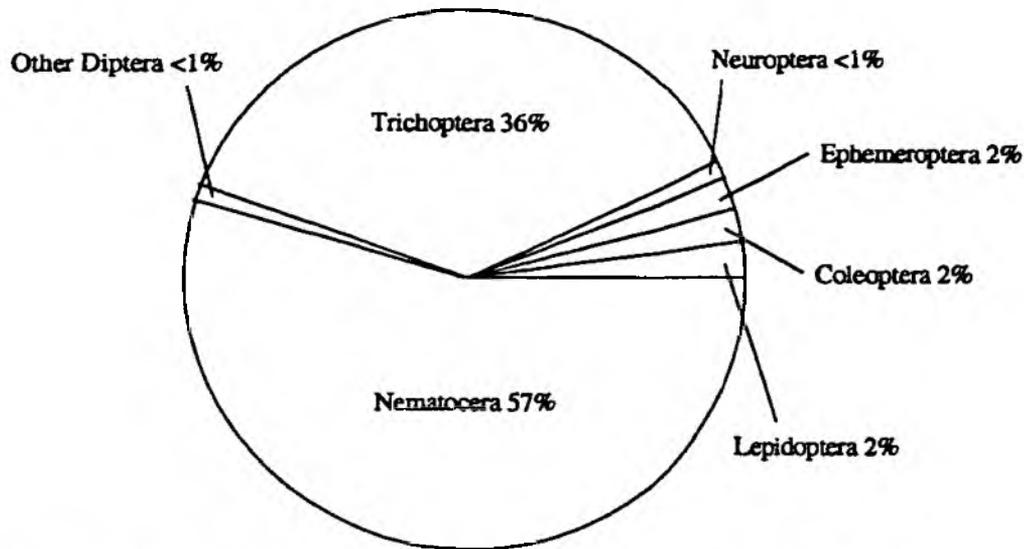


Figure 7.9 Insect taxa in the diet of Daubenton's bat (Swift and Racey 1983)

Rivers more than 9 m wide, which tended to be slow-flowing and supported abundant Trichoptera and Ephemeroptera, were selected in County Durham (Sargent 1991). The size of foraging area needs to be at least 0.5 ha (Nyholm 1965); no such estimate has been obtained for pipistrelle or Natterer's bats. The foraging activities of Daubenton's are significantly curtailed by winds greater than force 3, possibly due to the reduction in flying insects (Sargent 1991).

Natterer's bat

The diet of Natterer's bats is less well documented. They are foliage gleaners of riparian vegetation and do not often forage over the water itself (Poulton 1929). Prey items include Diptera, Coleoptera, Arachnida, larval stages of Lepidoptera, Muscidae and Anthomyiidae. Natterer's bats are selective predators, choosing larger individual prey items (Mayle 1990).

Pipistrelle

The foraging activity of pipistrelle bats rises in the hour following sunset and remains high for the following 3 hours (Sargent 1991). They feed on dense swarms of insects by flying up and down at the height of the thickest riparian vegetation for up to 20 minutes and then flying onto another feeding area. This method of feeding is termed 'trap lining'. If insect density is greater at any one point they remain there longer than usual. The distance between the bankside canopies dictates the area of open space in which the pipistrelle can easily forage, and it tends to be found along wider rivers with their greater air space (Sargent 1991). An exception occurs during high winds, when the pipistrelle shifts its foraging into more wooded (sheltered) areas – leading potentially to competition with Daubenton's bats.

Their opportunistic diet is comprised of mostly Nematocera (e.g. crane flies, midges) and Trichoptera; Lepidoptera and Coleoptera provide a smaller proportion of the diet; and Ephemeroptera and Neuroptera are taken when available (Poulton 1929, Swift *et al.* 1985). The pipistrelle bat shows no preference between foraging over pools and riffles, suggesting that this species is not affected by changes in insect density over these habitats, nor by

interference with echo-location. There is a minimum density of insects required for efficient feeding: if the density of insects is less than 0.3 m^{-3} then pipistrelles do not remain to forage in that area (Swift *et al.* 1985).

Whiskered bat

The whiskered bat emerges early in the evening and remains intermittently active throughout the night. It flies with a fluttering action at moderate speed, gliding for short periods whilst feeding below canopies on small arthropods gleaned from the foliage. Whiskered bats generally select narrower rivers (less than 9 m) with ample bankside vegetation of 1-5 m height (Sargent 1991).

7.6.5 Competition

Competition for food between different bat species is mostly avoided by different foraging strategies, and to some extent by specialization to different insect species and size group. Swift and Racey (1983) studied brown long-eared bats (*Plecotus auritus*) and Daubenton's bats. Although sharing the same roost, they emerged and returned at different times of the evening and morning. Unlike Daubenton's, long-eared bats foraged consistently within deciduous woodland, and although their diets consisted of the same taxonomic groups of insect, the proportions of each were markedly different.

During non-breeding periods, interspecific associations occur regularly among bats that use internal shelters. Most of these associations seem to be casual – perhaps due to the limited availability of roost sites, or due to shared temperature, moisture and darkness requirements. Gilbert and Stebbings (1958) found Natterer's, Daubenton's, whiskered and brown long-eared bats using the same cave as a winter hibernacula. Most species appear to use separate roosts during the maternity period; although exceptions include species that roost in different parts of the same shelter, such as brown long-eared and Daubenton's bats (Swift and Racey 1983).

Inter-specific competition for roost sites has been recorded; Mason and Stebbings (1972) observed displacement of noctule bats (*Nyctalus noctula*) by starlings in old woodpecker holes. Modern forest practices reduce the number of available holes by clearance of old and senescent trees, so competition for holes with other tree-using species could have an important effect on tree-roosting bats. Territorial aggression has been observed in Daubenton's bats when strong winds restrict the available foraging area (Mayle 1990) and intraspecific territoriality arises in pipistrelles when insect densities are low (Racey and Swift 1985).

8. DISCUSSION

8.1 Context

The review presented here represents a second step in the development of a national standard method of River Corridor Survey for the NRA; the first step having been the publication of the in-house report of the River Corridor Methodology Working Party. Both these publications adopt a habitat-based approach as the only realistic one available for a Catchment Planner/Conservation officer who is inevitably resource-limited and a river corridor surveyor who is inevitably time-limited. This habitat approach has, in reality, been the basis of the survey method ever since it was first developed by the Nature Conservancy Council, but the original habitats tended to be largely physical and the need for their recording was only obvious to more experienced surveys and ecologists. The current review has attempted to produce a more complete habitat listing and to justify the inclusion of as many habitats as possible from a review of the requirements of a large group of animal and plant species.

The species review presented here is entirely literature-based. We have avoided adding anecdotal comments from any sources. There is the inevitable risk that many studies reported in the literature are limited in scope or spatial relevance and thus can easily be taken out of context. Some may even be inaccurate. We feel it important that NRA review of this draft manuscript should highlight areas where our literature review does not match field experience, and vital that, in such cases, relevant experience should be documented as far as possible in the final report.

8.2 Levels of survey detail

The detail of ecological information needed for a river corridor almost always depends upon the management objective which first generated the information need. A proposal for regulation through the construction of an upstream reservoir will have a completely different impact, and hence information requirement, than a proposal for maintenance 'bushing' along a stretch of riverbank.

The habitat-based approach allows surveys to be tailored according to need. In the former example, attention would have to be paid to potential effects upon in-channel and edge habitats whilst in the latter, channel effects might be limited to a change in light regime but terrestrial corridor effects could be severe and survey work concentrated here. The development of a hierarchical system of survey approach; separating channel, margins, corridor, and floodplain, with habitat recording and mapping in each one, will enable the diverse requirements of River Corridor Surveys to be more effectively and consistently met.

8.3 RCS and computer databases

Rapid advances are currently being made in computer hardware and software, such that the time is not far off when each river surveyor could work from a laptop field computer pre-programmed with a question-and-answer survey system, and download data into Geographic Information Systems software mounted on each office desk-top PC for the analysis and presentation of survey results. This means for example, that within only a year or two a plant species list could be matched with the National Vegetation Classification in the field, or records of riffle-pool spacings compared with those expected from mean annual discharge.

These advances mean that the re-design of field procedures to achieve a standardised, high quality approach to River Corridor Survey needs to be flexible and open-ended. For that reason

the survey requirements suggested in this report are only presented as a comprehensive list rather than any more specific recommended format.

8.4 RCS and conservation evaluation

It is generally agreed that conservation evaluation is lagging behind survey and classification, with the only evaluation of river and riparian sites coming either from the terrestrial system, developed after the NCC's Nature Conservation Review and used for evaluation of NCR and SSSI status sites, or from fisheries science, where fish habitat assessment methods have been developed in both the UK and the USA (separate systems but both habitat evaluation).

We briefly reviewed fisheries evaluation in this project, because it requires habitat-based survey information and was therefore directly relevant. Conservation evaluation however, tends to be more species- and community-based and so it was not possible in the time available to explore the implications of a habitat-based survey approach to existing methodologies for conservation evaluation. A new NRA project will evaluate the most appropriate conservation evaluation needs; and together with a similar project launched by the Joint Nature Conservation Committee, this will bring RCS and conservation assessment together.

8.5 The way forward

There is no doubt that, if the underlying scientific basis is adequate, the recording of habitats in a River Corridor Survey is far more cost-effective than the recording of species wherever this is possible. There will always be a requirement for species information: for species which are used as habitat indicators; and for highly mobile species (such as birds or mammals) which either have a mosaic habit requirement or which are indicators of overall environmental health by virtue of their position at the top of food webs.

Specific recommendations for the advancement of RCS methodology and its application are made separately (page xiii of this report).

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9.2 Notes

A number of discrepancies between text and bibliography were found during preparation of this draft. Some remain – and are alerted below – but will be corrected before final revision of the report to incorporate NRA feedback from this draft.

1. Anderson (1989), Durska (1957), Thornton (1957), Plachter (1988), Sterling *et al.* (1992), Clemick *et al.* (1980) and Sargent (1984) are cited; but not listed in the bibliography [Chapter 2]
2. Thompson (1974) and Waters (1969) are cited; but not listed in the bibliography [Chapter 4]
3. Heggenes (1988) and Cunjak and Power (1986) are shown as having the same journal *et seq.* in the bibliography [Chapter 4]
4. Jost (1970), Parslow (1973), Pienkowski (1980), Pienkowski *et al.* (1980) and Tyler (1970) are cited; but not listed in the bibliography [Chapter 6]
5. Ormerod and Tyler (1987a,b) are not distinguished in the text [Chapter 6]
6. Ormerod and Tyler (1991a,b) are not distinguished in the text [Chapter 6]
7. Muller-Bohme (1936), Golley (1968), Birks (1981), Stoddart (1977) and Cuthbert (1967) are cited; but not listed in the bibliography [Chapter 7]
8. Lever (1978a,b) are not always distinguished in the text [Chapter 7]