Progress Report R&D Project 346

Physical Environment for
River Invertebrate Communities

University of Leicester
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1. LITERATURE REVIEW

Proper development of the project requires a review of existing and new information which is available through the scientific literature. Much of the relevant research is carried out abroad, notably in the USA and in continental Europe. There are also substantial programmes of research in Australia and South Africa. The review has three main aspects:

- Awareness of major and ongoing research programmes.
- Overview of the range of channel habitats and their ecology.
- Comprehensive reviews of specific topics.

1.1 Current awareness

The main method for maintaining current awareness has been direct contact with other groups. The Ecology Unit holds informal discusion meetings with groups such as the IFE and is represented at most major symposia (e.g. York 1990, Lund 1991, Barcelona 1992). Newly-published literature is regularly checked for relevant research reports: three major sources in this respect are Freshwater Biology, Hydrobiologia and Archiv für Hydrobiologie. The proceedings (Verhandlungen) of the International Association for Limnology also include a large amount of relevant information.

1.2 Overview

An overview of representative publications was prepared during spring/summer 1992 for its additional use as a contribution to R&D 291 [1]. The review is given here as Appendix A, and most of the referred material is available as hard copy. Fifteen main functional habitats were discussed, forming the basis for more selective reviews towards R&D 346.

1.3 Specific topics

The overview provides access points for existing information on channel habitats. We are now investigating selected topics in greater detail, to assess the results from this project in their proper context.

2. FIELDWORK

Determination of functional habitats from 'potential habitats' assumes that the range of variation within a potential habitat is realistically covered by a limited number of samples (we are using five). This requires that samples are taken from separate occurrences of each habitat, rather than being clustered around an access point; and thus requires work over a substantial length of river. It was originally intended to operate by 'courteous trespass', similar to Section 2.3 of the 1992 Draft RCS Guidelines prepared by the NRA.

It was sufficient to explain the purpose of the work if challenged on the River Smite, a lowland river with arable adjacent land-use and riverside public footpaths. A landowner on the River Dove (upland, adjacent pasture) objected strongly to uninvited entry to his land, and suggested that this would be a general reaction. In his particular case the immediate cause for concern was disease-free status of cattle, laid upon a broad dislike of public agencies. Similarly however, unsolicited work on most of the study rivers is unacceptable.

[1] Riparian and instream species-habitat relationships: Project Leader Richard Howell, Welsh Region.

A letter of apology was sent to the River Dove farmer[2]. We feel that to protect the interests of the Ecology Unit / NRA – and since personal injury is not out of the question – fieldwork on rivers other than the Smite cannot be undertaken without firm permission. A broadsheet explaining the reason for the work has been prepared (enclosed as Appendix B), for use with a covering letter in seeking permission. Landowners/tenants are difficult to contact during the day, due to the nature of their occupations; and it is difficult to write a satisfactory letter when neither name nor proper address are known. Richard Howell and Peter Barham suggested that we contact Operations and Fisheries staff of each Region to ask for contact names/addresses, and this is the line we are taking.

The programme of fieldwork for Summer/Autumn 1992 was curtailed by the problem of access; but this complies with our proposed development of the work, agreed in outline with the Project Leader.

3. PROJECT DEVELOPMENT

There are three key areas in which we feel the project should be continually open to review. These are working methods; scientific validity of the results; and the overall programme in the context of NRA R&D.

Field methods on the Anglian rivers (Welland, Wissey and Kym) placed great emphasis on discrete sampling of habitats. For example, shoots of emergent macrophytes were cut at the substratum surface and carefully removed to a hand-net. The objective of this – certainly realized – was to ensure that animals from other habitats were not sampled. However, such methods must also have undersampled uncommon species (small sample size) or those with efficient escape behaviour (much disturbance prior to capture). The August sampling on the River Smite supplemented intact samples with a timed sweep sample. We should analyse the results from the River Smite in comparison with those from the Anglian rivers, to assess the relative merits of the two approaches to sampling, prior to extensive further fieldwork.

The habitats which are present on a river in summer are far more diverse than their winter counterparts. For the most part this is not a problem, since the 'winter habitats' are a subset of the 'summer habitats' and some invertebrates pass the winter as life stages with a broad tolerance of environmental conditions. A substantial number of invertebrates have extended or even winter-based life cycles; and we should be looking at their habitats during the winter months (ideally January-February). We can get more detailed information on habitat use by quarterly sampling of a habitat-rich river (River Smite, which also offers ready access).

The programme for 1993/1994 has been specified in the PIA as field-testing of the work; but the nature of this remains undecided. The results of the work have relevance to both corridor surveys and water quality monitoring; as well as being useful in *ad hoc* decisions between management options. We recommend that fieldwork in the summer of 1993 should be a simultaneous effort on three lines:

- Sampling for analysis of functional habitats.
- Sampling for use of RIVPACS in water quality assessment.
- Corridor survey according to current NRA methodology.

The sampling for habitat analysis is that which was scheduled for summer 1993; but which we have been unable to carry out for reasons of access and a break in the drought. This will take advantage of the assessment of sampling methods detailed above.

[2] Mr Gould, Upper Whittle Farm, Longnor, Buxton, Derbyshire SK17 0PS

By applying biological water quality monitoring practices in concert with the habitat work, we will be able to address the issue of chemistry *versus* habitat in the use of RIVPACS predictions. Sampling will preferably be carried out by biologists from the NRA Regions, to the same protocol as routine biological monitoring. The Ecology Unit could do the sampling if necessary, but the results would not be as closely comparable with those of experienced in-house biologists.

Comparison of functional habitats with the coverage of river corridor surveys (RCS) will allow us to recommend adjustment to the methodology; or the erection of a further module as appropriate. In principle, it should be possible to estimate the RCS coverage of instream functional habitats from the NRA guidelines to RCS surveyors. In practice however, the implementation of RCS by Regions or their contractors will always vary to some degree, as will the emphasis on features by individual surveyors. For this reason it would be most useful to have RCS carried out by the usual surveyors.

Both of the points above will require some Regional input for their full value. Whilst aware that this can't be left until the last minute, we do not plan to negotiate any collaboration until Steering Group members have had sufficient opportunity to consider our proposed programme.

4. TIMESCALE

The programme which we propose for the remainder of R&D 346 is shown below, as Figure 4.1. The expected duration of each component is shown, together with the timing of significant outputs.

The precise timing of summer fieldwork will be influenced by Regional involvement, if this can be negotiated. It will be important to start the work during June, to guard against delays caused by heavy rain.

It is important that the Draft Final Report is available for NRA review during the timescale of the project, so that the other prescribed reports (R&D Report, Project Report etc.) can be compiled whilst the project worker is still applied to it full-time. This will avoid a lengthy delay between the draft stage and completion. R&D 346 funding terminates at the end of March 1994; but the NRA provided some flexibility in the transition from an earlier phase of the project, which we should recognise if necessary (i.e. full-time through April).

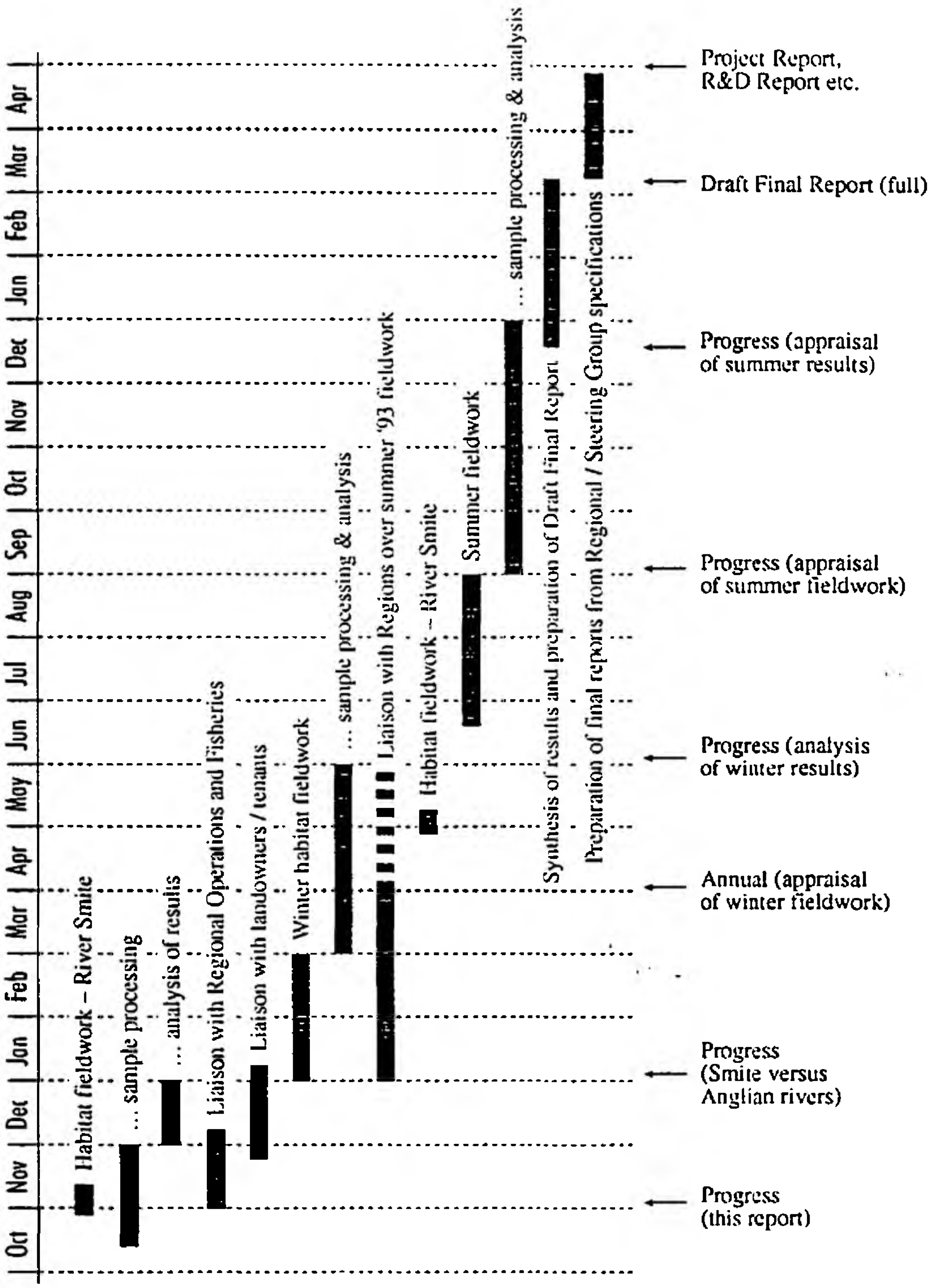

Figure 4.1 Proposed schedule for remainder of R&D 346

APPENDIX A – LITERATURE REVIEW

A.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.

A.1.1 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.

A.1.2 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.

A.1.3 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 *Epoicocladius 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.

A.1.4 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).

A.1.5 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.

A.2 <u>Background</u>

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 A.1). 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 A.1 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 (*Phalaris*)	Submerged fibrous systems of bankside stands
Ranunculus penicillatus	Extensive stands in regions of low current velocity, usually at margins of channel
Callitriche hamulata	As above
Potamogeton natans	As above

Table A.2 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 A.2). 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 A.3).

Table A.3 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
	Burrowers and crevice dwellers	Gathering collectors	Depositional FPOM
		Shredders	Depositional CPOM and macrophytes
Depositional (pools, margins, off-channel, side channel)	Sprawlers	Gathering collectors	Depositional FPOM
		Shredders	Leaf packs
	Burrowers	Gathering collectors	Depositional FPOM
		Shredders	Leaf packs, wood
	Climbers	Shredders	Vascular hydrophytes
		Piercers	Macroalgae

Replicated sampling from a non-exhaustive list of particulate and vegetative potential habitats was carried out by Bournaud and Cogerino (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 A.4) was validated by macroinvertebrate distribution, subject to varying overlap within three wider habitat classes of erosion, sedimentation and vegetation.

Table A.4 Habitat types on the River Rhône (Bournaud and Cogerino 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 A.5). Analysis using TWINSPAN (Hill 1979) showed 20 functional habitats (Table A.6), which were used to produce a surveyors' habitat checklist (Table A.7). 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 A.5 Potential habitats on the River Welland

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

Table A.6 Functional habitats on the River Welland

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

Table A.7 Habitat checklist for the River Welland

Gravel	Run – *Nuphar*	Margins – 'reeds'
Riffle	Pool – *Nuphar or Nymphaea*	– *Rorippa*
– with *Fontinalis*	– *Elodea*	– *Phalaris*
Silt – with leaf litter	– *Cladophora / Enteromorpha*	– *Agrostis*
– 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 A.8), representing the dominant river types identified by the IFE River Communities Project (Wright *et al.* 1984, 1989).

Table A.8 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	Itchen (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.

A.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 A.1).

The American Society of Civil Engineers (ASCE) combined hydraulic and biological information in a classification of bed material (ASCE 1992: see Table A.9); 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.

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 1970a). 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).

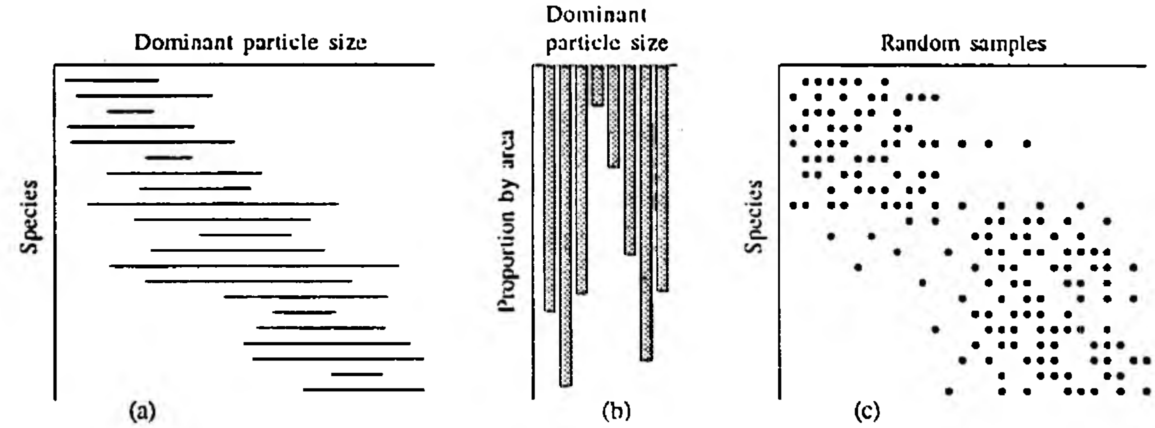

Figure A.1 Conceptual diagrams: 'random' particle-size tolerances (a) could still produce distinct communities (c), if the distribution of dominant particle-size is not unimodal (b).

Table A.9 Example of a bed-material classification (ASCE 1992)

Bed type	Particle size (mm)	Relative frequency of bed movement	Typical macroinvertebrate Density	Diversity	Fish use of bed sediments
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

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, *Centroptilum 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 hygropetric 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).

A.4 Aquatic macrophytes

A.4.1 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 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; 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 Ephydridae: 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 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 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.

A.4.2 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 A.10), 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 A.2b). 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 A.2a). 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.

Table A.10 Number of taxa found in habitats on River Welland (data: Smith *et al.* 1991)

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

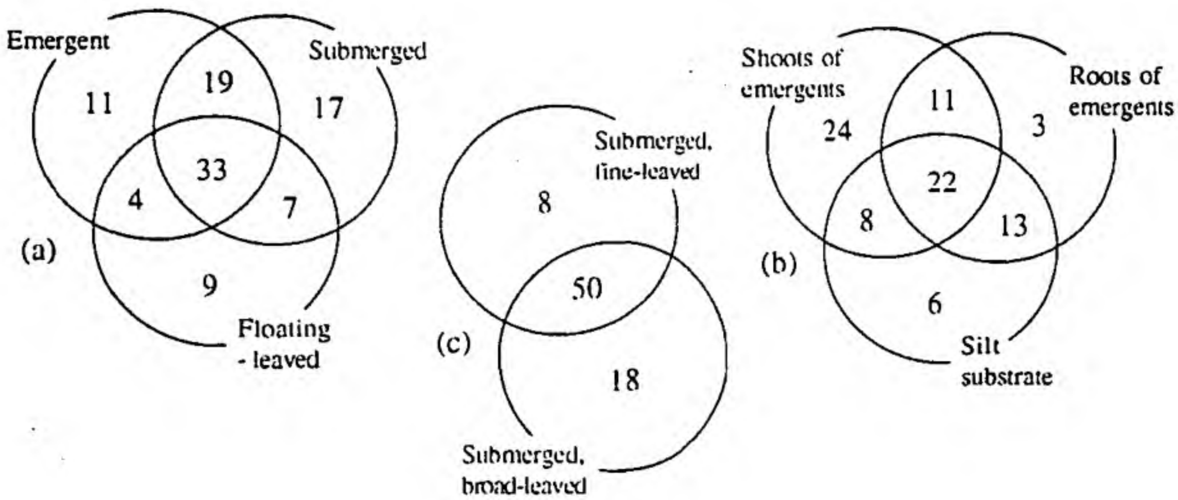

Figure A.2 Taxon richness of habitats on River Welland (data: Smith *et al.* 1991)

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 A.2c). 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.

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 (Egglishaw 1969, Thorup and Lindegaard 1977, Table A.10) 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 1970a) 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 pereger*; run, *Ephemerella ignita* and Orthocladiinae 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 (Bardonnet *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 A.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.

A.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 (Egglishaw 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.

Egglishaw (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 (Egglishaw 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. Conners 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.

A.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 (Egglishaw 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 woody 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.

A.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).

A.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.

A.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 Brönmak 1984, Brönmark and Malmqvist 1984), *Amphipsyche 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).

A.10 Habitat list

A preliminary list of in-stream functional habitats is given (Table A.11) based upon the discussions above.

Table A.11 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. *Sparganium* (usually grasses, rushes, reeds)
– Floating-leaved	Leaves lying on water surface, e.g. *Nuphar* and some *Potamogeton* species
– Submerged, broad-leaved	Include strap-like leaves of e.g. *Butomus* and *Sparganium emersum*
– Submerged, fine-leaved	Include fine leaves (e.g. *Zannichellia*) or dissected leaves (e.g. *Ranunculus*)
– Mosses	Aquatic types, e.g. *Fontinalis, Rhynchostegium*
– Macroalgae	'Cott', usually *Cladophora* and *Enteromorpha* on lowland rivers
– Marginal plants	Rooted around (e.g. *Phalaris*) or below (e.g. *Rorippa*) 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. *Alnus, Salix, Acer*
Exposed rock	Used instream by some filterers; and in wet places (hygropetric zone)

A.11 References

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Physical Environment for River Invertebrate Communities

Information Note

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BACKGROUND

We now have enough infomation to predict the animals (mayflies, shrimps etc) which should be in a river, from basic measurements of the channel and its water chemistry. These predictions are often compared with actual samples of the animals, to find out how clean the rivers are. The problem is that animals need certain 'habitats' (gravel, pools, water plants etc) as well as clean water. For example, if there are no slow-flowing parts there will be no dragonflies, however clean the water is. It is important to find out which animals are in which habitats, so that we don't say that clean water is polluted when really it's a habitat shortage.

Some time ago, dredging of the river (for land drainage and flood defence) was done with little care for the animals and plants. The laws have become stricter and stricter, until now the National Rivers Authority has to actually increase the conservation value of rivers. They still have a legal duty to control flooding, but the people who plan engineering work have to be more careful. Sometimes money is available directly to restore damaged rivers to a more natural state. To take more care in flood defence work, and to make best use of money for restoration, we need to know how 'good rivers' work – so they can be copied.

THIS PROJECT

The NRA have funded us (Leicester University) to provide some of the information which is needed about river habitats. Ten rivers have been chosen which best show the range of 'river types' in England and Wales –

River	Reach (Grid references)	River	Reach (Grid References)
Dove	SK 084 665 - SK 146 504	Itchen	SU 523 325 - SU 470 233
Swale	NY 885 015 - NZ 146 007	Yorkshire Ouse	SE 467 621 - SE 591 455
Wansbeck	NY 996 844 - NZ 119 850	Hampshire Avon	SU 163 174 - SZ 158 933
Torridge	SS 324 178 - SS 542 064	Evenlode	SP 202 312 - SP 274 197
Teifi	SN 684 628 - SN 217 437	Smite	SK 690 262 - SK 773 427

On each of these rivers we need to do a quick survey, to find out which habitats are present. Then we need to take samples of the animals in each habitat, and look at them back at the laboratory to find out what types they are.

Each habitat type has to be sampled in several places, to make sure that the differences we see between them aren't just by chance. If you pull an orange from one bag of fruit and an apple from another, that doesn't tell you much – but if you pull 5 oranges from one bag and 5 apples from another, you can say more surely what's in them.

USE OF THE RESULTS

Knowing which animals have definite habitat needs will prevent us from making mistakes about measuring water quality. We'll be able to tell whether species-poor samples are the result of pollution, or the result of missing habitats.

When we know which habitats are important, these can be used to help surveyors make their notes. Rivers which have good habitats can be identified for careful protection, and rivers with habitat problems can be the first targets for restoration effort. There's only so much money available for restoration work, but we'll know how to use that money most effectively.

NOTES