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THE MACROINVERTEBRATE FAUNAS OF RIFFLES AND POOLS

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Abstract—Macroinvertebrate data from studies of rivers, principally in upland areas, of North America (9) and U.K. (8) were examined to identify differences in the faunas of riffles and pools. Overall the number and representation of taxa in the two habitats was similar although some organisms (e.g. *Simulium*, riffles; *Corixa*, pools) may characterise each habitat. Significantly higher mean total densities were detected in riffles compared to pools and this confirmed the general conclusions from a number of individual studies: significantly higher densities in pools were never reported. The relative abundance of major groups (Orders) in each habitat was variable: in general, Ephemeroptera formed a higher proportion of the total density in riffles than pools and the reverse was found for Diptera. Only the Ephemeroptera showed significant differences in density between the two habitats, riffles supporting higher densities than pools. Considering families, only Baetidae and Simuliidae showed significant differences in density, riffle density being greater than pool density. Community analyses, commonly used in biological surveillance, indicated that it is unlikely that major misclassification of sites will result from the use of data collected from one habitat (riffle/pool) only. Further studies are required at lowland sites to test the general applicability of the conclusions.

INTRODUCTION

Biological surveys are generally designed to detect temporal and spatial patterns in populations and communities and may aid in the assessment of damage to biological resources caused by pollution or physical disturbances (Edwards *et al.*, 1975). For the purposes of ecological surveillance it is both impracticable and unnecessary to study all facets of the biological community in any environment. Hellawell (1978) has provided a comprehensive and critical appraisal of the relative merits of studying different organisms in lotic waters and concluded that, in general, biological signals derived from the macroinvertebrate community are the most useful: other workers (Hynes, 1965; Roback *et al.*, 1969) support this conclusion.

Obvious practical constraints related to methods have usually restricted macroinvertebrate sampling in rivers and streams to the relatively shallow riffle areas which are easily accessible by wading and which many workers regard as relatively homogenous habitats (Needham & Usinger, 1956). This is clearly reflected in the development of sampling techniques (Hellawell, 1978) and there are relatively few methods generally suitable for use in the deeper, slower flowing, reaches of rivers. Some assessment of the performance of deep water samplers has been undertaken recently (Elliott & Drake, 1981a, b) but generally there are few descriptions of the macroinvertebrate fauna of pools available in the literature.

Yang (1971) details the development of riffle and pool sequences in lotic waters and broadly defines riffles as having steeper, and pools shallower, water surface slopes than the average of the sequence. In particular, upland areas with steep bed gradients are characterised by riffle (fast-flowing, eroding) and pool (slow-flowing, depositing) sequences and studies in the upper R. Severn indicated that the relative ratio (by surface area) of riffles: pools was about 0.4 (Newson & Harrison, 1978). However, the hydraulic characteristics of such upland areas are likely to reduce the physical differences between riffles and pools at high flows. Of course, in lowland reaches of rivers riffles are restricted in distribution and, because of the physical characteristics of the river channel, riffles and pools are more discrete and greater differences between faunas may occur. Unfortunately relevant data are not readily available and most published comparisons of the fauna of riffles and pools are restricted to upland rivers with stony substrata. However, the variation in channel size and the physical characteristics of pools and riffles in these studies is substantial. Thus, reported channel widths range from a few metres to 45 m and reported riffle and pool depths range from 5 to 35 cm and 15 to 300 cm respectively.

Clearly if there are substantial differences between the macroinvertebrate faunas characterising riffles and pools the restriction of sampling effort to the riffle habitat may provide a poor overall description of the macroinvertebrate community of the river. This review considers published and, where available, unpublished comparisons of the macroinvertebrate faunas of riffles and pools and attempts to identify major overall differences between them.

Table 1. Studies of macroinvertebrate communities in riffles and pools used in the analysis (r = riffle; p = pool)

Reference	Sampling season	River		Sampler
1. Surber (1937)	Jan.–Feb.	Shenandoah and Potomac	USA	Surber (36 mesh)
2. Wene & Wickliff (1940)	Jan.–Oct.	Blacklick creek	USA	Basket (36 mesh)
3. Lymen & Dendy (1943)	Oct.–Nov.	Holston	USA	Surber (r) Petersen dredge (p)
4. Briggs (1948)	Oct.–June	Stevens creek	USA	Surber
5. O'Connell & Campbell (1953)	July–Aug.	Black	USA	Surber
6. Gaufin *et al.* (1956)		Lythe creek	USA	Surber (r) Ekman grab (p)
7. Egglishaw & Mackay (1967)	Apr. and Oct.	Shelligan burn	UK	Surber (24 and 48 mesh cm^{-1})
8. Mundie (1971)	Apr.	Small creek	Canada	"Box" (50 μm aperture)
9. Armitage *et al.* (1974)	May, Aug., Oct.	Tees	UK	Kick (255 μm aperture)
10. Hughes (unpublished) (1975)	July	Cynon	UK	Surber (24 mesh cm^{-1})
11. Armitage (1976)	May, June–Dec.	Tees	UK	Artificial substrate (255 μm aperture)
12. Hynes *et al.* (1976)	June	Hirnant	UK	Kick & standpipe corer (130 μm aperture)
13. Minshall & Minshall (1976)	Feb.	Mink creek	USA	Hess (263 μm aperture)
14. Pollard (unpublished) (1977)		Cynon	UK	Surber (250 μm aperture)
15. Scullion (unpublished) (1977)	Nov.	Taff Bargoed	UK	Hess (480 μm aperture)
16. Rabeni & Minshall (1977)		Mink creek	USA	Artificial substrate (490 μm aperture)
17. Wisniewski (unpublished) (1978)	June	Wye	UK	Hess (r) Pumped Hess (p) (440 μm aperture)

DATA SOURCES

Most of the earliest published descriptions of the macroinvertebrate faunas of riffles and pools were undertaken in the U.S.A. (Table 1) but more recent sources of unpublished data have been made available to the authors from research programmes undertaken by the University of Wales Institute of Science and Technology in south and central Wales. Full descriptions of the rivers are not always available but most investigations were carried out in relatively small rivers, usually in upland reaches where riffle–pool sequences predominate. Information on water quality is available only for rivers from the U.K. The upper catchment of the R. Wye and R. Tees are unpolluted and generally base-poor, particularly the R. Wye (Armitage, 1976; Oborne *et al.*, 1980) whereas the R. Taff Bargoed and R. Cynon in industrial south Wales are subject to pollution from a number of sources. Contaminants include suspended particulate material which may be of particular significance when comparing the fauna of eroding (riffle) and depositing (pool) habitats.

SAMPLING METHODS AND DATA PROCESSING

The sampling methods are described in the relevant publications and theses and are not considered in detail here. Comparisons of the macroinvertebrate faunas were made between adjacent riffles and pools and most workers used a Surber sampler, or equivalent device ("Hess"; "box"), which collected macroinvertebrates from a fixed area of substratum (Table 1). Armitage *et al.* (1974) and Hynes *et al.* (19[illegible]) used a pond net and collected "kick" samples and artificial substrates were used in other investigations (Wene & Wickliff, 1940; Armitage, 1976; Minshall & Minshall, 1976; Rabeni & Minshall, 1977).

In most studies the same method was used in riffles and pools but in three investigations (Lymen & Dendy, 1943; Gaufin *et al.*, 1956; Wisniewski, 1978) different methods were used to sample each habitat. Sometimes the differences in technique were small: for example, Wisniewski (1978), studying riffles and pools in the upper R. Wye in Wales, used different collecting procedures with a Hess or cylinder sampler. In riffles (depths, 13–21 cm) the capture of macroinvertebrates depended upon current velocity (53–60 cm s^{-1}) washing organisms into a downstream net whilst in pools (depth, 36–46 cm), where current velocity was lower (0–39 cm s^{-1}), water was pumped out of the sampler into a net. It is unlikely that such variations in method lead to major distortions in the description of the composition or abundance of organisms. However, studies which compare the faunas of riffles and pools on the basis of different methods, one of those being an artificial substrate, have not been included in this analysis since artificial substrates have been shown to selectively collect some benthic macroinvertebrates (Hughes, 1975b; Shaw & Minshall, 1980) and relative differences between habitats were likely to be spurious. Where the same artificial substrate has been used in each habitat the study has been included.

There are also other problems in making comparisons between studies: in particular these arise from:

(i) The selection of organisms by mesh size: mesh size was not always reported in the studies considered (Table 1).

(ii) The collection of samples at different times of the year which is likely to influence the qualitative and quantitative composition of the sampled fauna (Murphy, 1978).

(iii) The varied taxonomy used by different workers. For example, in some of the earlier studies (Lymen & Dendy, 1943) animals were identified to Order only whilst in more recent investigations (Pollard, 1977; Scullion, 1977; Wisniewski, 1978) more detailed identification, to species where possible, was attempted.

(iv) Differences in fauna are likely to reflect substrate type and stability but it was impossible to adequately consider such variables in the present analysis.

In order to reduce such errors comparisons have been based upon paired data from adjacent riffles and pools, each riffle and pool forming a pair in the statistical analysis. Therefore, comparisons are based upon information collected at the same time with generally similar efficiency. In particular the paired t-test has been used to test the general hypothesis that there is no significant ($P < 0.05$) difference between faunas in riffles and pools. Where necessary data have been transformed to log x or log ($x + 1$). In addition, bias, resulting from taxonomy unique to any particular study, in community analyses has been restricted by "masking" the data set.

RESULTS

Taxonomic representation

All of the Orders of aquatic macroinvertebrate reported in all the 17 studies were represented in both riffle and pool habitats and a paired comparison (t-test) indicated that there was no significant difference between the number of Orders and families recorded in riffles and pools. The total number of taxa recorded from riffles and pools varied considerably between studies (riffles, 21–105; pools 16–100) principally because of the substantial differences in taxonomic penetration between investigators and the natural characteristics of each site. Nevertheless no difference was established, on the basis of paired comparisons, between the total numbers of taxa recorded in the two habitats. However, results may be site specific and Scullion (personal communication), in a study not included in the overall analysis, found significantly higher numbers of taxa in a riffle, compared to an adjacent pool, of an impounded river in Wales: no such differences were established in a nearby naturally flowing river. Armitage (1976) recorded highest numbers of taxa in pools in the impounded R. Tees.

More than 70 families were recorded in all studies but only 6 (Haplotaxidae, Piscicolidae, Helodidae, Sialidae, Lepidostomatidae, Blepharoceridae) and 5 (Coenagriidae, Corixidae, Gyrinidae, Odontoceridae, Stratiomyidae) were restricted to riffles and pools respectively.

The number of taxa restricted to either riffles or pools was 38 and 27 respectively (Table 2) but there was considerable variation between investigations. Hynes *et al.* (1976) in a study of a small stream in Wales recorded 15 taxa in riffles only and none restricted to pools whilst Armitage *et al.* (1974) found that in Pennine streams more taxa were unique to pools (17) than riffles (7): Pollard (1977) reported 18 taxa collected only from riffles and 21 restricted to pools.

Overall only 6 taxa were restricted to one habitat in more than one study: *Hydropsyche siltalai*, *Protonemura meyeri*, *Narpus* spp and *Rhyacophila munda* in riffles and *Perlodes microcephala* and *Phagocata* sp. in pools (Table 2). Such an analysis is clearly constrained by the limited number of comparisons between riffles and pools since several organisms apparently restricted to the latter habitat (Table 2) —e.g. *Perlodes microcephala*, *Ecdyonurus venosus* and *Phagocata* sp.—have been collected from general surveys of riffle macroinvertebrates, e.g. Brooker & Morris (1980).

However, some other groups, restricted to either riffles or pools in only one of the studies reviewed, have a more understandable basis to their distribution and may be characteristic of the different habitats considered. Several species of *Simulium* were restricted to riffles (Table 2) and the distribution of these organisms, and also Hydropsychidae, has been shown to be influenced by current velocities (Edington 1965; Phillipson, 1957; Philipson & Moorhouse, 1974). Most molluscs (other than *Ancylus*) and the dytiscid beetle, *Oreodytes*, were restricted to pools as were: *Callicorixa* (Hemiptera), *Corixa* (Hemiptera), *Pyrrhosoma* (Odonata) and *Gyrinus* (Coleoptera).

Numerical density

The ratio (riffle:pool) of mean total densities of macroinvertebrates recorded from all studies varied from 11.5 to 0.5 with an overall ratio of 1.1 (Table 3). Paired comparisons of mean densities at each study site showed that, overall, the density of macroinvertebrates supported in riffles was significantly greater than in pools ($t = 3.8$, $P < 0.005$; $n = 21$; after log x transformation). This analysis supports the conclusions of some individual studies (Table 1–study codes: 7, 10, 11, 14, 15, 17): there are no reports of pool densities being significantly higher than riffle densities.

In the studies considered, the Ephemeroptera, Oligochaeta and Diptera generally formed the greatest proportion of the total density of macroinvertebrates, these three groups contributing between 38–98% and 24–97% of the density in pools and riffles respectively. In some studies other groups were relatively abundant, principally Trichoptera (maximum 47%), Coleoptera (47%), Plecoptera (34%), Malacostraca (64%) and Mollusca (52%). Scatterplots of the proportions of these major groups in riffles and pools indicate considerable variability in the relationship (Fig. 1) but nevertheless there is a general indication that the relative abundance of some major groups is often similar in riffles and pools.

Overall only Ephemeroptera had significantly ($t = 3.0$, $P < 0.01$, $n = 16$; after log x transformation) higher densities in riffles compared with pools and this group often formed a higher proportion of the riffle fauna than the pool fauna (Fig. 1b). In contrast, the proportion of Diptera was generally greatest in pools (Fig. 1b) although the densities of this group in

Table 2. Taxa restricted to either riffles or pools in the studies reviewed. North American studies are asterisked

Rifles		Pools	
Taxon	Study code	Taxon	Study code
Piscicola geometra	10		
Nais communis	14	*Phagocata*	8*, 17
Pristina idrensis	15	*Trocheta subviridis*	14
Haplotaxis gordioides	15	*Nemoura cinerea*	11
Leuctra nigra	11	*Perlodes microcephala*	14, 17
Protonemura meyeri	11, 12	Ephemeridae	5*
Nemoura cinctipes	16*	*Ecdyonurus venosus*	11
Perla bipunctata	17	*Siphonoperla lacustris*	11
Pteronarcys	13*	*Hydroptila tineoides*	14
Isoperla fulva	16*	*Melamophyla marcureus*	14
Baetis niger	14	*Odontocerum albicorne*	14
Siphonoperla torrentium	12	*Agabus*	14
Hydropsyche siltalai	15, 17	*Oreodytes rivalis*	10
Stenophylax lateralis	14	*Oreodytes septentrionalis*	17
Lepidostoma hirtum	17	*Gyrinus*	14
Rhyacophila munda	13*, 17	*Helophorus affinis*	17
Potamophylax latipennis	12	*Microtendipes*	14
Narpus	8*	Stratiomyidae	13*
Narpus concolor	13	Tabanidae	14
Limnophila	8*	*Chrysops*	8*
Blepharoceridae	8*	*Pyrrhosoma nymphula*	14
Chironomus lugubris grp.	14	*Corixa*	14
Corynoneura celtica	14	*Callicorixa woolastoni*	11
Orthocladius rivulorum	15	*Spherchon verrucosa*	14
Potthastia longimana	17	*Lymnaea truncatula*	11
Tanytarsus	17	*Physa fontinalis*	14
Procladius	17	*Sphaerium corneum*	17
Pedicia	11	Planorbidae	8*
Simulium cryophilum	12		
Simulium monticola	17		
Simulium rheophilum	12		
Simulium tuberosum	12		
Sialidae	14		
Unionicola	8*		
Helodidae	14		
Hygrobates longipalpis	14		
Lebertia insignis	14		
Malaconthrus	8*		

the two habitats were not significantly different. Scullion (personal communication), in a study of the R. Wye in Wales not considered in detail in this analysis, found that riffle densities of Ephemeroptera were greater than pool densities and the reverse was the case for Coleoptera: other groups showed no significant differences in density estimates.

Significant differences in the density of families in riffles and pools were established for the Baetidae [$t = 2.19$, $P < 0.05$, $n = 14$; after log $(x + 1)$ transformation] and Simuliidae [$t = 5.14$, $P < 0.01$, $n = 9$; after log $(x + 1)$ transformation] only and densities were always greatest in riffles.

Egglishaw & MacKay (1976) reported that pools supported higher densities of ecdyonurids (Ephemeroptera) in spring and that riffles had higher densities in autumn, suggesting that migration occurred prior to the emergence of these organisms as adults. Armitage *et al.* (1974) did not confirm this finding in collections from the R. Tees. However, Boon (1979) has suggested that older larvae of *Hydropsyche* migrate from riffles to pools prior to emergence and Armitage (1976) reported significant differences in the distribution of size-classes of mayflies in riffles and pools in the R. Tees: the larger nymphs of *Baetis rhodani*, *B. scambus* and *Caenis rivulorum* being more abundant in pools whilst smaller nymphs were more abundant in riffles.

Wisniewski (1978) found significantly higher densities of larvae of *Rheotanytarsus* sp. (Chironomidae) in the pool of a riffle–pool complex at one site only in the upper Wye. The larvae were predominantly early instar and this distribution may reflect the oviposition behaviour of the adult: no differences in densities between habitats were found at two nearby sites where only later instars were collected.

Biomass density

Relatively few workers have compared the biomass of macroinvertebrates in riffles and pools (Table 3).

Table 3. Total numerical (No. m^{-2}) and biomass (in parenthesis where available, g wt m^{-2}) density of macroinvertebrates in riffles and pools

Study code		Density Riffle	Density Pool	Ratio Riffle:Pool	
1	(Shenandoah)	2820 (34.5)	431 (5.4)	6.5	(6.4)
1	(Potomac)	990 (28.0)	861 (38.8)	1.2	(0.7)
2		1378	344	4.0	
3		2435	211	11.5	
4		267 (10.0)	83 (1.9)	3.2	(5.3)
5		1003 (1.9*)	652 (1.0*)	1.5	(1.9)
7		11.566 (11.4)	6994 (9.4)	1.6	(1.2)
8		44,765	26,966	1.7	
10		2584	4903	0.5	
11		156,357	140.831	1.1	
12		318.878 (6.2)	327.731 (13.8)	1.0	(0.4)
13		22,855	21,253	1.1	
14†	(i)	464	574	0.81	
	(ii)	502	203	2.4	
	(iii)	3487	5125	0.7	
	(iv)	4568	717	6.4	
15		11,392	3448	3.3	
16		6581	3284	2.0	
17†	(i)	803	335	2.4	
	(ii)	1476	920	1.6	
	(iii)	9724	6691	1.4	

*Converted from dry weight.
†Results from different sites.

Generally fresh weights have been reported but where only dry weights are available (O'Connell & Campbell, 1954) these have been converted to fresh weight on the basis of the ratio (wet:dry weight) of 3:1 (Hynes, 1970). Molluscs have been included. Using the few data available no significant overall difference was established between macroinvertebrate biomass in riffles and pools. Ratios of biomass (riffle:pool) varied from 0.4 to 6.4 (Table 3).

Community structure

Many measures of community structure have been used to describe lotic macroinvertebrate faunas and these are reviewed in detail by Hellawell (1978). Where basic data are available—chiefly from unpublished studies undertaken in south and central Wales—and there is some consistency in the level of identification, community indices have been computed.

There was no overall difference in the Shannon–Weiner Index (Hellawell, 1978) computed for riffle and pool faunas using data from studies in the U.K. (Table 4). Using the same basic data, similarity indices based upon the Jaccard coefficient (which reflects

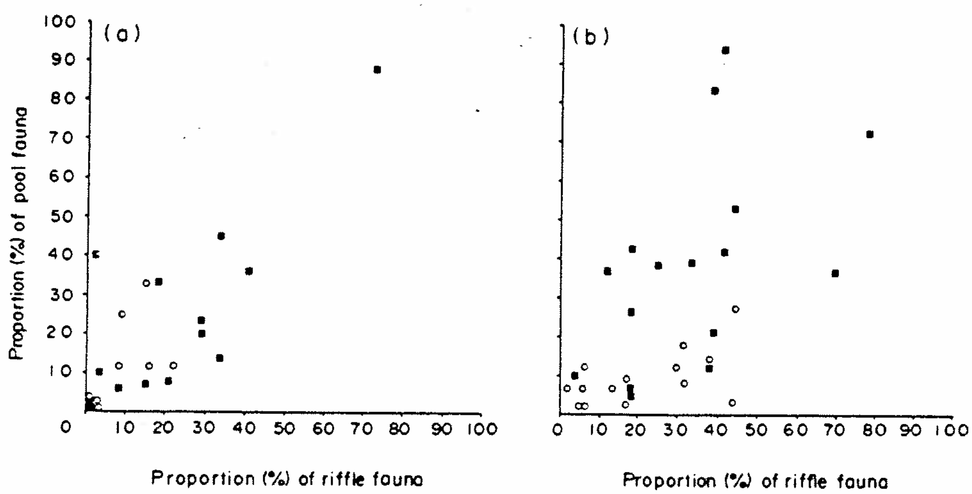

Fig. 1. The relationship between the relative abundance (%) of (a) Oligochaeta (■) and Plecoptera (○) and (b) Diptera (■) and Ephemeroptera (○) in riffles and pools.

Table 4. Shannon–Weiner Index ($\log_e$) computed for riffles and pools. From studies in the U.K.

Study code	Riffles	Pools
10	3.72	3.84
11	1.87	1.76
14 (i)	4.19	4.22
(ii)	2.88	3.75
(iii)	2.28	2.33
(iv)	3.03	2.06
15	1.95	2.46
17 (i)	3.25	3.08
(ii)	3.28	2.90
(iii)	3.24	3.54

presence and absence only) and Kendall's rank correlation coefficient (which takes account of the relative abundance of taxa) were computed for each habitat (riffle/pool) at all sites and analysed by average linkage clustering (Fig. 2). However, to reduce the risks of discriminating collections of invertebrates from specific studies on the basis of taxonomy unique to any particular investigation (e.g. the use of unconfirmed morphological features to separate taxa in studies 10, 14, 15 and 17) taxa not recorded in more than one river were excluded from the Jaccard analysis. For the computation of Kendall's rank correlation coefficient only those taxa occurring at two or more sites and comprising 1% or more of the total site density were included in order to reduce errors of spurious correlation based upon mutual absences.

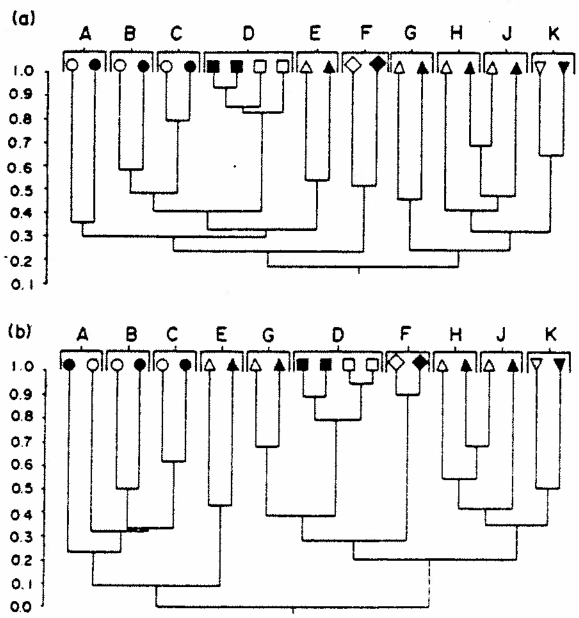

Fig. 2. Average linkage clustering of (a) Jaccard coefficient and (b) Kendall's correlation coefficient. Open symbols, riffles; solid symbols, pools. Sites A, B and C, R. Wye; D, R. Tees; E, G, H and J, R. Cynon (Pollard, 1977); F, R. Taff; K, R. Cynon (Hughes, 1975a).

Both analyses (Fig. 2) indicated that riffles and pools at the same site were generally more closely related to each other than to other riffles and pools respectively, even within the same river system. However, in the R. Tees in the North of England (D, Fig. 2) riffles at nearby sites clustered together and pools likewise formed a group. At site J, the R. Cynon in south Wales, the riffle fauna is most closely associated with the pool of site H on the same river, probably because site J was subjected to high loads of silt from a coal washery and this may have influenced the pool fauna (where deposition occurred) more than the riffle fauna (Pollard, 1977). On the basis of the correlation analysis the riffle and pool at site A on the Wye do not appear to be closely associated and cluster with the riffles and pools of sites B and C but this cannot be readily explained.

Additionally, as might be expected, sites (each comprising a riffle–pool pair) were generally more closely associated within rather than between rivers (Fig. 2). Rivers of similar characteristics—unpolluted, upland—also clustered together and analyses using both Jaccard and Kendall indices indicated that the riffle–pool pair at site E (R. Cynon) was closely associated with Wye and Tees sites reflecting the relatively unpolluted nature of the Cynon site (Pollard, 1977).

GENERAL CONCLUSIONS

This analysis of macroinvertebrate data from a variety of investigations carried out in North America and the U.K. is inevitably restricted by the different techniques used for biological collections and the seasonal differences in the descriptions. However, the precautions employed during data manipulation should have reduced such influences and it is unlikely that any major pattern of differences in the characteristic faunas of riffles and pools has not been detected. Nevertheless, probably as a result of the limited methods available for sampling deep, slow flowing rivers and the natural distribution of riffles and pools, comparative studies of these latter habitats are generally restricted to upland rivers and streams. Clearly further studies of the fauna of lowland rivers are an urgent requirement.

Several important points emerge from the comparison of the macroinvertebrates of riffles and pools. Overall the representation of taxa (Orders, Families, species-groups) in the two habitats is generally similar. There are certain taxa which are probably characteristic of riffles (e.g. *Simulium* spp) and pools (e.g. *Corixa*) but other taxa which were restricted in their distribution to one habitat in the studies considered are known from the literature to occur in the other.

It is clear from this analysis and from some individual studies that the total density of macroinvertebrates in riffles is significantly higher than in pools, the overall ratio (riffles:pools) being 1.1. In no study was the reverse relationship detected. Overall the composition of the fauna, by major taxonomic group, from all studies was generally similar, probably reflecting the upland location of the study sites. However, ephemeropteran densities were significantly higher in riffles than in pools, although density differences were not detected in other groups. Additionally, Ephemeroptera appeared proportionally more abundant in riffles whilst Diptera formed a higher proportion of the fauna in pools than riffles.

The established qualitative and quantitative differences in macroinvertebrate fauna between riffles and pools, which may be influenced seasonally by the migrations of certain organisms, are unlikely to substantially bias the overall description derived from samples collected from one habitat—in practice riffles. This is reflected in the analyses of community structure from which it is possible to draw important conclusions in relation to biological surveillance programmes. Results indicated that the discrimination of pattern in these biological collections was not impaired by the use of samples collected exclusively from one habitat (riffle/pool). Thus, riffles and pools at the same site generally clustered together rather than with similar habitats at other sites. Additionally, where sites were most closely associated with sites from other catchments (e.g. site E with sites A, B, C and D, see Fig. 2) with respect to their faunas there was often an underlying environmental similarity. However, there was evidence that the effects of pollution by particulate solids were greater on the pool fauna than the riffle fauna and the use of a riffle habitat for the detection of such forms of pollution may result in a loss of sensitivity.

It can be concluded that, although differences in taxonomic representation and abundance can be detected between the faunas of riffles and pools of upland rivers, the bias introduced by sampling only one habitat is unlikely to lead to misclassification of sites in biological surveillance programmes. However, where information on aspects other than spatial patterns is required, e.g. estimates of productivity, some cognizance of differences in abundance between habitats is required.

Additionally it is important to recognise that insufficient data are available to extend these general conclusions to lowland rivers where the physical characteristics of riffles and pools may be considerably more discrete than at upland sites. Data collected from lowland (within about 30 km of tidal limit) rivers under the auspices of the Analysis of River Communities in Great Britain Project (see Furse *et al.*, 1981) indicated site differences in the distribution of taxa between riffles and pools (Table 5). At two sites in the R. Forth in Scotland the number of taxa in riffles was substantially greater than the number in pools and this was reflected in those taxa restricted to each habitat. Similar numbers were recorded in riffles and pools in the Wansbeck, confirming the general conclusion of the analysis of upland studies, and it may be that differences in sampling technique in riffles (kick sampling) and pools (grab sampling) in the Forth restricted the collection of fauna in the latter habitat. Overall, there were few families occurring at relatively high densities which were restricted or characteristic of riffles or pools. In general the Philopotamidae and Simuliidae were found only in riffles and Haliplidae and Dysticidae were characteristic of pools, confirming some of the results of the analysis of upland rivers. Nevertheless further studies in lowland rivers are urgently required to better assess differences in the macroinvertebrate faunas of riffles and pools.

Table 5. Comparison of the numbers of macroinvertebrate taxa in riffles and pools of two lowland rivers in the U.K. (data provided by P. D. Armitage)

Taxa	R. Forth (Two sites)	R. Wansbeck (One site)
Total (riffles)	118	73
Total (pools)	76	79
Restricted to riffles	68	33
Restricted to pools	26	39

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