

With very best wishes
Ted Wise

Studies on the Ephemeroptera of a Northumbrian river system

I. Serial distribution and relative abundance

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Summary

The River Coquet is a clean, fast flowing, moderately calcareous river. It is young to mature in development and supports a typical torrential fauna. Marked trends in successional replacement along the river course are confined to the scarce species of Ephemeroptera and the absence of longitudinal zonation in the distribution of some common species is related to the topographical characteristics of the system. A distinct successional trend by one species is attributed to its intolerance to the lower temperatures at high altitudes. Major discontinuities in distribution are found between the Ephemeroptera of the main river and certain tributaries. The paucity of certain otherwise abundant species in one region is related to silt deposition resulting from sand and gravel excavation.

Introduction

In Britain a comparatively large number of general river surveys have appeared in which the Ephemeroptera are included as part of the entire invertebrate fauna. (These include: Percival & Whitehead, 1929, 1930; Whitehead, 1935; Butcher, Longwell & Pentlow, 1937; Jones, 1940 *et seq.*; Badcock, 1949; Hynes, 1961, 1968; Maitland, 1964, 1966; Morgan & Egglisshaw, 1965; Egglisshaw, 1964, 1969; Egglisshaw & Morgan, 1965; Arnold & Macan, 1969; Langford & Bray, 1969; Minshall & Kuehne, 1970; Learner *et al.*, 1971; Edwards *et al.*, 1972; Mills & Smith, 1974.) In addition a number of more specialized field

studies on the distribution of the Ephemeroptera have been described. (These include: Harker, 1953; Macan, 1957; Collins, 1971; Langford, 1971.) Few of these studies have attempted to explain, except in very general terms, the distributions they describe and many have been restricted to either small hill streams or to localized sections of large rivers.

This report describes a preliminary survey of the distribution and relative abundance of Ephemeroptera nymphs in the River Coquet, Northumberland, England. It is intended as a contribution to the existing knowledge of stream ecology and in particular the biology of the Ephemeroptera. It is also intended to increase the data available on the freshwater fauna of an area in north eastern England which, with the exception of the Trichoptera (Phillipson, 1957, 1962; Edington, 1965, 1968; Bray, 1966), the amphipod and isopod Crustacea (Sutcliffe, 1972), and the Ephemeroptera (Burleigh, Wise and Gray, 1972), has received little attention in the past.

The River Coquet system

Topography

The River Coquet rises in the Cheviot Hills 1450 ft (441.88 m) above sea level, close to the Scottish Border (Fig. 1). It flows eastward through a varied geological succession for a distance of some 50 miles (80.47 km) and enters the North Sea at Amble on the Northumberland Coast. The Coquet has a catchment area of 569.3 km² and is the largest of several parallel rivers which drain the region of uplift between the major systems of Tyne and Tweed. It is a rain-fed spate river, young to mature in development. The valley sides are steep, tree cover is sparse and land drainage is good. Consequently run-off is rapid causing violent floods of short duration.

The river can be divided into three main topographical regions (Fig. 2).

(i) *The upper 'hill' region* extends for 20 miles (32.19 km). The valley is unfenced hill grazing land

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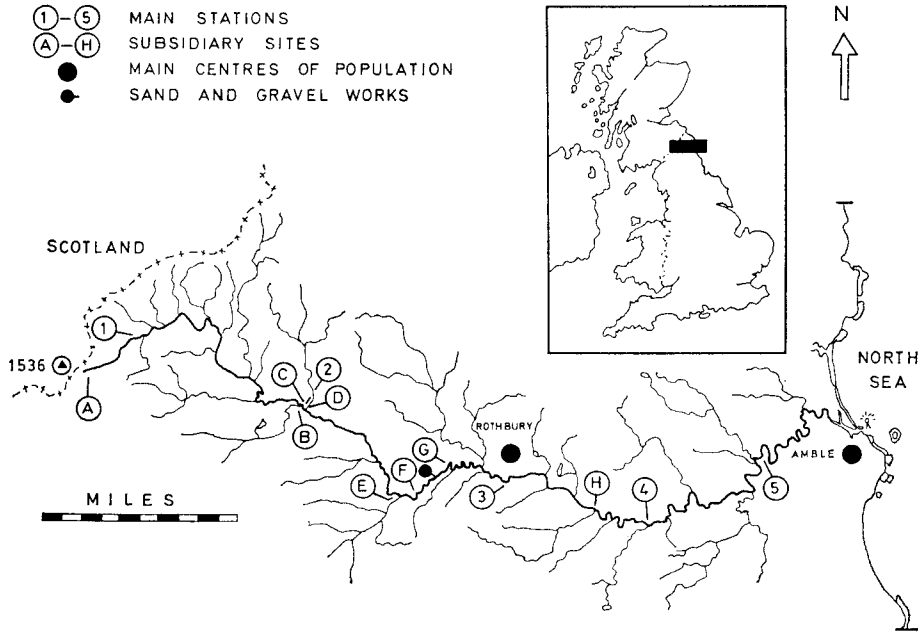


Fig. 1. The River Coquet system. Sites of sampling stations.

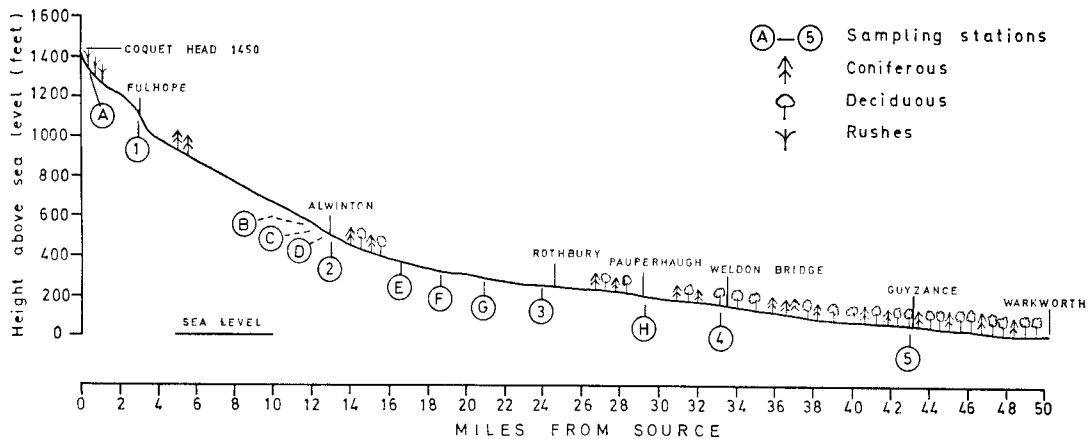


Fig. 2. The River Coquet system—main river profile.

and consists of smooth steep-sided hill slopes covered by coarse grasses (dominant *Nardus stricta* L.). The river is small and fast flowing with a steep gradient (fall 350.42 m in 32.19 km; or 10.9%). The substrate consists of bare stones, boulders and bedrock with *Fontinalis antipyretica* Hedw. and *Hypnum* sp. as the dominant plants. Bank vegetation is sparse consisting of *Juncus effusus* L. and there is no tree cover.

(ii) The 'middle' region extends for just over 6 miles (9.66 km) and has a more level gradient (fall 13.72 m in 9.66 km or 1.4%). The river is broad and mainly shallow following a meandering course through an alluvial flat. The substrate consists mainly of bare stones with deposits of sand and silt in places. Bryophytes are sparse, *Ranunculus fluitans* Lam. occurs where the substrate is suitably shallow and where silting exists beds of *Elodea canadensis* Michx. are

established. Marginal vegetation is sparse and tree cover is restricted to a few willows (*Salix* spp.) and alders (*Alnus glutinosa* (L.)). The open valley bottom provides some rich arable land.

(iii) *The lower 'coastal plain' region.* The river falls steadily (fall 76.20 m in 37.0 km or 2.1 %) for the last 23 miles (37.0 km) of its course to the upper limit of tidal influence at Warkworth. It is broad and shallow with a fast flowing current. The substrate consists of bare stones except where artificial conditions are induced by a series of man-made weirs. *Ranunculus*, *Fontinalis* and *Cladophora glomerata* (L.) Kutz. are the dominant aquatic plants. Marginal vegetation is dominated by deciduous trees. The land is used principally for arable farming.

Geology

The 'hill' region is dominated by a deeply dissected volcano of Old Red Sandstone age. A great mass of granite lying centrally is surrounded by pyroxene—andesites which cover the majority of the volcanic area. The whole igneous complex (outcrop 22% of catchment area) has been exposed to considerable weathering and is covered by a blanket of glacial drift.

The 'middle' Coquet, bounded by coarse and massive Fell Sandstones to the south, flows through a region noted for the Cementstone Group (outcrop 19% of catchment). A second escarpment of Fell Sandstone (combined outcropping 18% of catchment) forms a barrier between the Cheviots and the 'coastal plain'. This is interrupted by faulting allowing the Coquet to cut a gorge through to the 'coastal plain'.

From here the dip continues to fall eastwards away from the central Cheviots and the river crosses a series of outcrops. The most important of these are a belt of Middle Carboniferous Limestone and an outcrop of Millstone Grit (combined outcropping 21% of catchment). The whole area has been affected by glaciation and the solid geology of the 'coastal plain' has been largely obscured by thick deposits of drift and morainic material, belonging to the period of ice retreat.

Climate

The climate of the Coquet valley is typical of north-eastern England and is, in general, rather cold and comparatively dry.

Observations on climatic conditions are based on

recordings of the meteorological station at Acklington (55° 18' N 01° 38' W) between 1945 and 1969. During this period the average air temperature varied from 3.0°C in January and February to 14.1°C in July. The average annual rainfall was 64.8 cm.

Temperature regime

Water temperatures were measured by a series of maximum—minimum thermometers situated at Stations 1–5 and at subsidiary sites A, B, C and E (Fig. 1). Recordings were taken at monthly intervals between October 1967 and April 1969.

Additional information was provided by two Cambridge mercury-in-steel thermographs sited at Stations 1 and 5. Continuous temperature recordings were made immediately above the stream bed between March 1968 and August 1969.

The highest temperature (22.8°C) was recorded at Station 1 during June 1968. The lowest temperature (–0.6°C) was recorded on several occasions between January and March in both 1968 and 1969 at all the main river stations.

In summer the range in temperature was greatest in the 'hill' region (maximum range 5.6–22.8°C, in June 1968). Summer temperatures were more conservative in the 'coastal plain' (maximum range 8.3–18.3°C, in June 1968). Winter temperatures were less variable throughout the length of the river (maximum range –0.6–7.8°C, in January 1968).

The conservative temperatures (maximum range 3.3–11.1°C, in November 1968) recorded at Site A are characteristic of a spring source.

The buffering effect of marginal tree cover on the temperatures of tributary streams is demonstrated by a comparison between the Barrow Burn, at Site B (maximum range 7.2–16.7°C, recorded in June 1968) and the River Alwin, at Site C (maximum range 6.1–21.7°C, recorded in June 1968).

Detailed information on the temperature regime of the Coquet will be published separately.

Water quality

Hydrogen-ion concentration. pH determinations were made using a portable field meter. Measurements were taken on a seasonal basis (i.e. during March, July and November of 1968) from all tributaries at a point immediately prior to their confluences with the main river. Measurements were also taken from the main river immediately above and below each confluence.

Under low water conditions pH values were always high and remarkably constant throughout the river system (range 7.7–9.1). However, under flood conditions pH values were reduced (range 7.0–7.5).

Dissolved oxygen. During 1969, dissolved oxygen determinations were made on a seasonal basis, using a portable field meter.

Oxygen saturation never fell below the range 93–102% and there was no indication of oxygen depletion, at any time, throughout the entire length of the river.

Chemical characteristics. Water samples were taken from Stations 1–5 on a seasonal basis (Table 1). All chemical analyses were carried out in accordance with the methods of Mackereth (1963). An E.E.L. flame photometer was used for Sodium (Na^+) and Potassium (K^+) determinations.

Table 1. Chemical characteristics of the River Coquet (summarized data for period October 1967 to October 1968)

	Station 1	2	3	4	5
Calcium (mg/l)	32.0	18.5	29.5	31.0	34.0
Magnesium (mg/l)	6.5	10.0	5.7	6.5	6.7
Sodium (mg/l)	9.5	6.5	10.5	12.5	10.5
Potassium (mg/l)	3.4	0.5	3.6	3.0	3.3
Alkalinity (mg/l CaCO_3)	82.5	55.5	68.0	70.0	69.0
Alkalinity (mEquiv./l HCO_3^-)	1.65	1.11	1.36	1.40	1.38
Chloride (mEquiv./l)	0.08	0.20	0.17	0.19	0.22
Nitrate + sulphate (mEquiv./l)	0.32	1.06	1.00	0.93	0.92

The general chemical characteristics (e.g. calcium hardness, range 18.5–34.0 mg/l Ca^{++} and alkalinity range 55.5–82.5 mg/l CaCO_3^-) are closely related to the geology of the watershed. High values in the lower reaches (Stns. 4 and 5) are also attributed to the richness of the land in the coastal plain. Lower values at Station 2 are a result of dilution by the Barrow Burn which is relatively poor in dissolved salts. More detail on the effects of geology on the chemistry of water bodies in Northumberland may be found in Sutcliffe (1972).

Low nitrate (range 0.10–1.00 mg/l $\text{NO}_3\text{-N}$) and ammonia (range 0.00–0.33 mg/l $\text{NH}_3\text{-N}$) values, supplied by the former Northumbrian River Authority, reflect the pure quality of the water throughout the length of the river.

River flows

Long term discharges have been recorded (in cumecs) by the Northumbrian River Authority in

the upper 'hill' region (NT 870083) between 1957–69 (lowest daily mean 0.105, average 1.281, peak 33.960) and in the lower 'coastal plain' (NU 230045) between 1966–69 (lowest daily mean 1.533, average 10.797, peak 207.184). Mean current velocities, measured using an Edington flow meter 1 cm above the surface of the substrate, were variable in space and time at all stations (range 5 cm/s to 50 cm/s).

Pollution and water abstraction

The non-tidal river is clean throughout its length. The only appreciable centre of population (1700) is at Rothbury where a sewage treatment plant is operative.

The River Coquet is an important source of water for potable supply, an average abstraction of some 9 million gallons per day being made from the non-tidal river at Warkworth Dam.

Fisheries

The Coquet is one of the most important game fishing rivers in the North of England and has good spawning facilities for migratory fish. Records from the Northumbrian River Authority counting station at Warkworth between 1959 and 1970 show an average yearly run of 12 615 sea trout (*Salmo trutta* L.) and 2810 salmon (*Salmo salar* L.).

General conclusions

The Coquet is a moderately calcareous river, free from any significant sources of pollution or enrichment. The benthic invertebrate communities are typically 'rhithron' in character and larval Ephemeroptera, Plecoptera, net-spinning Trichoptera and Simuliidae are the dominant forms. It provides a useful comparison with some of the less productive rivers of the Lake District and other regions of Britain.

Sampling stations

Five main sampling stations were established along the main river course, at approximately equal intervals (Fig. 1).

Stations 1 (National Grid Reference NT 816102, elevation 1100') and 2 (NT 920056, eln. 500') represent the 'hill' region, Station 3 (NU 048016, eln. 225') the 'middle' region and Stations 4 (NZ

137984, eln. 150') and 5 (NU 207030, eln. 50') the 'coastal plain' region.

Subsidiary collecting sites were established at the main river source, on certain tributaries and other places of special interest (Fig. 1).

Site A (NT 776077, eln. 1450') at Coquet Head. The river rises at an altitude of 1450 ft (441.88 m) from a raised *Sphagnum* bog. The watercourse is a small channel which flows rapidly through a flattish area at the head of the watershed. The substrate consists of small stones and peat. Marginal vegetation consists of *Juncus effusus* and *Nardus stricta* grassland.

Site B (NT 918059, eln. 500'). The Barrow Burn rises 1150 ft (350.42 m) above sea level and drains the rough moorland Fell Sandstone hills on the south side of the watershed. It is about 7 miles (11.26 km) long and joins the River Coquet at Alwinton. At Site B, the stream is fast flowing, with boulder-strewn cascades and peat-stained pools. Vegetation is mostly absent and the watercourse is heavily shaded by alders.

Site C (NT 922056, eln. 500'). The River Alwin is 8 miles (12.87 km) long, rises 1750 ft (533.40 m) above sea level and drains the andesite hills on the north side of the Coquet valley. It joins the Coquet (in close proximity to the Barrow burn confluence) above Alwinton Bridge. At Site C, the Alwin leaves its steep sided valley and flows rapidly across a flattish area to its confluence with the Coquet. The substrate is composed entirely of bare stones and large marginal banks of shingle are deposited by winter spates.

Site D (NT 921056, eln. 500'). The Hosedon Burn rises 1100 ft (335.28 m) above sea level. It drains the south-facing andesite hills of the watershed and joins the River Alwin immediately above its confluence with the main river. At Site D it is a narrow channel flowing swiftly through a flat *Juncus* bog. *Fontinalis* grows on the more stable areas of a predominantly stony substrate.

Site E (NY 974998, eln. 350'). The Grasslees Burn drains the moorland Fell Sandstone area of the south side of the upper watershed and its highest tributaries rise at altitudes of over 1000 ft (304.80 m) At Site E it is characterized by a series of peat-stained pools shaded by alders.

Site F (NY 983999, eln. 325') lies on the main river immediately upstream of Castron, a broad shallow area where sand and gravel is removed from the river bed. Site G (NU 008023, eln. 300') lies on the main river below Castron. Conditions at both

sites are similar with eroded stony substrates usually associated with rapid current velocities.

At Site H (NZ 102994, eln. 200'), situated on the 'coastal plain' region of the main river, conditions are similar to those described for Stations 4 and 5.

Methods of study

Methods of sampling the bottom fauna of stony streams are reviewed by Macan (1958), Cummins (1962) and Ulfstrand (1968). Some of these techniques are also reviewed by Frost, Huni & Kershaw (1970) in their critical appraisal of a kicking method, similar to that employed by Hynes (1961). The method employed for the present investigation was a modified combination of those techniques used by Macan (1957) and Hynes (1961).

Samples were obtained by means of a 12 meshes per cm square-framed net with 25 cm sides. The net was positioned between the operator's feet and an area of substrate (25 cm × 100 cm), immediately upstream of the net, was thoroughly excavated to a depth of about 20 cm using a rake. Organisms disturbed by this procedure were swept into the net by the current. Large stones were removed by hand and washed into the net. A 10-min period was taken to complete a series of twenty such sub-samples. These together constituted one collection which sampled an approximate area of 5 m². Although restricted to shallow water, this method can be operated under adverse and variable conditions and provides comparable results on a relative basis. It is considered that the use of the rake and the denudation of measured plots improves both efficiency and sample accuracy.

The distribution of Ephemeroptera nymphs

Twenty-three species of Ephemeroptera are recorded in the present survey. In contrast to the findings of other workers (e.g. Ide, 1935; Macan, 1961; Kamler, 1967) the largest number of species were found in the upper reaches of the Coquet. However, there was no marked successional replacement of abundant species along the main river course and discontinuous distributions were confined to the scarce species. The most marked discontinuities were found in certain tributaries.

Main river stations

The results are expressed as the annual total number of individuals of each species, taken from each station at monthly intervals, between October 1967 and September 1968 (Table 2). The species can be conveniently grouped according to their distribution and abundance.

Group 1—Abundant species with continuous distributions. Of the three most abundant species *Baëtis rhodani* was dominant. It occurred in large numbers at all stations except Station 3. Although present in smaller numbers, the nymphs of *B. muticus* followed a similar pattern. The nymphs of *B. scambus* (Etn.) and *B. fuscatus* are taxonomically indistinguishable but, as the latter prefers calcareous conditions, Macan (1970) considers them to be ecologically distinct. In support of this contention all adult material examined from the Coquet proved to be *B. fuscatus*. It achieved its greatest numbers in the lower Coquet at Station 5 and there was a significant reduction in numbers at Station 3.

Rhithrogena spp., the second most abundant taxon, was well represented at all stations. The nymphs of *R. semicolorata* are indistinguishable from those of *R. haarupi* (Macan, 1970). Although all final instar nymphs collected during April and May, which

emerged in the laboratory, proved to be *R. semicolorata*, circumstantial evidence suggested that *R. haarupi* was also present. Thus a group of large robust nymphs (max. length 16 mm), with an emergence period in March, were thought to be *R. haarupi* (see Kimmins, 1972). These were distinct from a group of smaller nymphs (max. length 10 mm), with an emergence period during May and June, which proved to be *R. semicolorata*.* From the numbers of nymphs remaining in the benthos after the emergence of *R. haarupi*, it was concluded that *R. semicolorata* was most abundant in the upper reaches whereas *R. haarupi* was most abundant further downstream. These observations are in agreement with those of Macan (1970).

Ephemerella ignita, the remaining dominant species, was present in large numbers at all stations. It did, however, show a sequential increase in numbers proceeding in a downstream direction, being most abundant at low altitudes.

The nymphs of *Centroptilum luteolum* occurred in their largest numbers at Station 1. They were present in comparatively small numbers at the lower stations where they may have been confined to the less

* Details of seasonal distributions and life histories will be published separately.

Table 2. Serial distribution and relative abundance of Ephemeroptera nymphs in the River Coquet

	Station 1	2	3	4	5	Total
Group 1—Abundant species with continuous distributions						
<i>Baëtis rhodani</i> (Pict.)	1120	1021	164	1386	1424	5115
<i>Rhithrogena semicolorata</i> (Curt)/ <i>R. haarupi</i> (Esb. Pet)	963	1061	845	1517	564	4950
<i>Ephemerella ignita</i> (Poda)	272	164	610	814	1035	2895
<i>Ecdyonurus torrentis</i> Kimmins	253	124	48	124	145	694
<i>B. fuscatus</i> (L.)	130	107	16	90	284	627
<i>Centroptilum luteolum</i> (Müll.)	363	46	76	24	68	577
<i>E. dispar</i> (Curt.)	86	67	50	79	132	414
<i>B. muticus</i> (L.)	128	91	11	56	108	394
<i>Caenis rivulorum</i> Etn.	63	174	30	20	35	322
<i>E. venosus</i> (Fabr.)	132	93	17	8	10	260
<i>Ecdyonurus</i> spp. indet.	47	24	3	12	10	96
Group 2—Scarce species with discontinuous distributions						
<i>Heptagenia lateralis</i> (Curt.)	87	26	17	1	0	131
<i>Ephemerella notata</i> Etn.	0	0	9	4	19	32
<i>Paraleptophlebia submarginata</i> (Steph.)	17	6	0	0	0	23
<i>H. sulphurea</i> (Müll.)	0	0	0	2	19	21
<i>Habrophlebia fusca</i> (Curt.)	17	2	0	0	0	19
<i>Baëtis niger</i> (L.)	2	6	3	0	0	11
<i>Siphonurus lacustris</i> Etn.	1	1	0	0	0	2
<i>Centroptilum pennulatum</i> Etn.	2	0	0	0	0	2
<i>Proclæon pseudorufulum</i> Kimmins	0	1	0	0	0	1
<i>Caenis horaria</i> (L.)	0	0	0	0	1	1
Total	3683	3014	1899	4137	3854	16587

Values given are the annual total number of individuals taken between October 1967 and September 1968.

accessible areas of deposition. Similarly *Caenis rivulorum* was apparently most abundant at Station 2 and occurred in relatively small numbers in the lower reaches.

Three species of the genus *Ecdyonurus* were present in the Coquet system and observations on their distributions are based on the numbers of larger nymphs which could be identified with confidence. *E. torrentis*, the dominant species, was most abundant at Station 1 but, contrary to the findings of other workers (e.g. Macan 1957; Maitland, 1966), it was not confined to the small stream channels of the upper valley. Similarly *E. venosus* was common and relatively abundant in the 'hill' region—especially at Station 1. Although not excluded from the lowland river it was only present in very small numbers. *E. dispar* was relatively common and abundant throughout the main river, but achieved its greatest expression in the lower Coquet, tending to replace *E. venosus* at Stations 4 and 5. A marked reduction in the numbers of ecdyonurids at Station 3 was similar to that already described for the baëtids.

Group II. Scarce species with discontinuous distributions. *Paraleptophebia submarginata* and *Habrophlebia fusca* only occurred at Stations 1 and 2 and were most abundant at Station 1. There is, therefore, strong evidence that these species were confined to the 'hill' region. Similarly *Centroptilum pennulatum*, *Procloëon pseudorufulum* and *Siphonurus lacustris* were restricted to the upper 'hill' region. *Baëtis niger* was restricted to the upper and middle reaches and achieved its greatest abundance at Station 2. Since the Barrow Burn enters the Coquet immediately above Station 2 it is possible that the abundance of *B. niger* at this point was a consequence of stream drift (see Site B).

In contrast *Ephemerella notata* was limited to the 'middle' and 'coastal plain' regions. It was most abundant at Station 5 and followed the same general trend in distribution as *E. ignita*.

The most interesting discontinuity in longitudinal distribution and a classic example of successional replacement was exhibited by the two members of the genus *Heptagenia*. *H. lateralis* was the most abundant species and occurred in greatest numbers at Station 1. It appeared to phase out at Station 4 and was excluded from the lower 'coastal plain' region. Conversely *H. sulphurea* was confined to the 'coastal plain' region and attained its greatest numbers at Station 5. As the overlap between these species coincided precisely with the outcrop of Carboniferous Limestone which characterizes the 'coastal

plain', there is, therefore, evidence to support the view held by Macan (1961) that *H. lateralis* replaces *H. sulphurea* in non calcareous areas. One individual of *Caenis horaria* was obtained from Station 5. This is typically a still-water form (Macan, 1970).

Subsidiary stations

Sites F and G. The influence of sand and gravel extraction at Caistron. The apparent paucity of Ephemeroptera nymphs at Station 3, in particular those belonging to the genus *Baëtis*, has already been described.

Topographical factors do not seem sufficient to explain this phenomenon. There is, however, a sand- and gravel-extracting company operating at Caistron, several miles above Station 3. The adverse effects of the deposition of suspended inorganic sediments on stream faunas, caused by sand and gravel washings etc., have already been noted (e.g. Stuart, 1959; Cordone & Kelly, 1961; Hamilton, 1961; Chutter, 1969). Consequently samples were taken at Site F (above) and Site G (below) the Caistron sand and gravel works (Table 3). Ranges in levels of suspended solids

Table 3. Samples from Sites F and G (6 May 1968) Compared by χ^2 test

Species	Site F	Site G	P Value	
<i>Rhithrogena semicolorata/haarupi</i>	540	231	<0.001	***
<i>Baëtis rhodani</i>	183	48	<0.001	***
<i>B. muticus</i>	60	19	<0.001	***
<i>Centroptilum luteolum</i>	14	0	<0.001	***
<i>Ecdyonurus torrentis</i>	22	12	>0.05	N.S.
<i>Heptagenia lateralis</i>	9	10	>0.05	N.S.
<i>E. venosus</i>	1	4	SUM	>0.05
<i>Siphonurus lacustris</i>	4	0		
<i>Caenis rivulorum</i>	2	0		
<i>B. niger</i>	1	0		
Total	836	324	<0.001	***

*** = very highly significant.
N.S. = not significant.

for Sites F and G were 1–10 mg/l and 1–60 mg/l respectively. χ^2 test revealed a very highly significant difference ($P = <0.001$) between samples, thus providing strong evidence that gravel extraction had at least a localized influence on the Ephemeroptera of this region. This influence did not affect all species to the same extent. Thus *B. rhodani*, *B. muticus*, *Rhithrogena* and *Centroptilum luteolum* were found to be intolerant ($P = <0.001$) but no reduction ($P = >0.05$) could be shown for the remaining species.

The profile of the main river suggests that settlement was probably minimal at G owing to the steep gradient but solids carried in suspension were more likely to accumulate at Station 3. Hence this may be one factor limiting the Ephemeroptera populations in the 'middle' region.

Sites A, B, C, D and E. Samples, taken from each subsidiary site on a seasonal basis, revealed certain departures from the trends reported for the main stations (Table 4).

Table 4. Occurrence of Ephemeroptera nymphs at subsidiary sites A, B, C, D and E

No. of Collections	Sites					Total
	A	B	C	D	E	
Group 1—Species common to Sites B and C or abundant at C						
<i>Rhithrogena semicolorata/haarupi</i>	0	277	551	51	0	879
<i>Baëtis rhodani</i>	13	63	611	97	13	797
<i>Ecdyonurus venosus/torrentis</i>	0	70	73	30	56	229
<i>Ephemerella ignita</i>	—	14	104	3	26	147
<i>Caenis rivulorum</i>	0	1	68	1	7	77
<i>B. muticus</i>	4	5	32	2	0	43
<i>B. fuscatus/scambus</i>	—	15	10	1	5	31
<i>Heptagenia lateralis</i>	2	0	9	1	0	12
Group 2—Species only present at Site B						
<i>Centroptilum luteolum</i>	3	28	0	2	35	68
<i>B. niger</i>	5	27	0	0	2	34
<i>Paraleptophebia submarginata</i>	0	8	0	0	1	13
<i>Habrophlebia fusca</i>	0	2	0	5	6	9
<i>Procloëon pseudorufulum</i>	0	2	0	0	2	4
<i>C. pennulatum</i>	0	0	0	0	3	3
<i>Leptophebia vespertina</i> (L.)	0	1	0	0	0	1
Total	27	513	1458	193	156	2347

The collection taken at Site A indicates quite clearly the scarcity of all Ephemeroptera nymphs at Coquet Head. Similar results obtained by Maitland (1966) show that the majority of species abundant in the River Endrick were absent from the extreme upper reaches.

The Barrow Burn and the River Alwin (Sites B & C), two important tributaries which flow into the same region of the Coquet, are markedly different in the species composition of their mayfly faunas (similarity 50%). The Barrow Burn was characterized by a large diversity of species but only small numbers of individuals. The species composition of the River Alwin was less diverse but some species were represented by very large numbers of individuals.

Baëtis rhodani, dominant in the main river, was also the most abundant species in the River Alwin.

The near exclusion of this ubiquitous species from the Barrow Burn is therefore of interest. As it has already been established that *B. rhodani* exhibits a positive phototactic response (Hughes, 1966; Thorup, 1966) it might be expected to avoid the heavily shaded areas of the Barrow Burn. Similarly *B. muticus* was comparatively abundant in the River Alwin but was replaced by *B. niger* in the Barrow Burn. *B. fuscatus/scambus* was apparently scarce in both tributaries. Species present in both tributaries, but most abundant in the River Alwin, include *Rhithrogena semicolorata*, *Ecdyonurus torrentis*, *Ephemerella ignita* and *Caenis rivulorum*. In contrast *Centroptilum luteolum* was absent from the Alwin but comparatively abundant in the Barrow Burn. The remaining species *Paraleptophebia submarginata*, *Habrophlebia fusca*, *Leptophebia vespertina* (L.) and *Procloëon pseudorufulum*, were all scarce and were only taken in samples from the Barrow Burn.

Samples taken from the Hosedon Burn (Site D) revealed similarities (80%) with those from the River Alwin. The sparsity of the summer population, however, was undoubtedly a reflection on the tendency for this stream to dry up during this period.

Grasslees Burn (Site E), in addition to being similar in character to the Barrow Burn, was similar (71%) in the composition of its mayfly populations.

The spatial distributions of nymphs at Site H were the subject of a special investigation which will be described in a separate publication.

Notes on additional species

The following is a summary of information on additional species with sporadic distributions which were recorded during the present survey but not included in the routine sampling programme.

Ephemerella danica Müll. A few individuals of *E. danica* were obtained from two tributaries, the Blackburn and the Debden Burn. Since this species was formerly common and abundant it may still occur elsewhere in the watershed.

Ameletus inopinatus (Etn), Macan (1970) states that *A. inopinatus*, the only arctic-alpine ephemeropteran known to occur in Britain, is confined to high altitudes and is common and abundant in becks above 1000 ft. The absence of this species from the upper Coquet was, therefore, somewhat unexpected. However, its presence in the upper reaches of the River Alwin (eln. 1750 ft) was revealed in June 1969 and it had already been reported in the Kidlandlee Dean, a tributary of the Alwin, by Sutcliffe (1972).

Discussion

Longitudinal zonation of benthic invertebrates has been described in earlier studies on running water systems (e.g. Dodds & Hisaw, 1925; Ide, 1935; Macan, 1957; Maitland, 1966).

The majority of attempts to classify river systems according to the type of zonation they display are based largely on the species of fish present (e.g. Huet, 1959, 1962).

However, Illies & Botosaneanu (1963), in their combined scheme for the classification of running water bodies, were able to distinguish well-defined topographical zones based on the composition of the bottom fauna communities. Of these 'rithron' and 'potamon' were considered of major importance. On the other hand Thorup (1966), in a critical review of studies of stream zone systems, concluded that it was not possible to construct a satisfactory classification on the basis of bottom fauna communities. Owing to the large number of variable factors, it would appear that precisely defined zones are of limited value. However, the existence of a transition in faunal types from source to mouth is an ecological phenomenon of some importance in most river systems. The absence of any well defined zonation of the abundant species of Ephemeroptera in the Coquet is, therefore, of great interest.

Topographically the Coquet is 'rithron' in character throughout its length and at its present stage in development it is a 'young' to 'mature' system. Thus there is no extensive flood plain with the associated fauna diagnostic of an 'old' river system (see Macan, 1957; Huet, 1962).

Apart from the availability of dissolved substances, the most marked changes that occur with decreasing altitude are increases in both water volume and marginal tree cover. It is suggested that these differences may be responsible for certain discontinuities, described for the scarce species of both the upland and lowland communities, as a function of temperature. They are thus confined to regions of tolerance whereas the ecological requirements of the abundant species are fully satisfied by the range of variable parameters experienced along the river course.

In considering seasonal distribution a distinct trend becomes apparent. Those species (i.e. *E. ignita*, *E. notata*, *E. dispar* and *B. fuscatus*) only present as nymphs in the benthos during the summer months, were more abundant in the lower reaches. However, certain of the 'winter' species (i.e. *Heptagenia*

lateralis, *Ecdyonurus venosus*, *E. torrentis* and possibly *Rhithrogena semicolorata*) were most abundant in the upper reaches. There is thus a possibility that these limitations are also temperature-dependent. Temperature as a factor limiting the distribution of the Ephemeroptera has already been observed by other workers (e.g. Macan, 1960, 1961). An experimental investigation of the effects of temperature on the distributions of certain ephemeroptera nymphs in the Coquet will be published separately.

Finally it was found that local distribution was subject to spatial discontinuities. This will also be the subject of a separate publication.

In conclusion it would appear that the absence of change in the topographical features of the River Coquet is of primary importance in determining the uniformity of its faunal characteristics. This is due principally to the influence of topographical factors on the flow regime and in consequence the nature of the substrate. The effects of thermal and chemical relationships are superimposed on this general scheme.

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