

## Life history patterns of river invertebrates

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### Abstract

The initiation of invertebrate distribution patterns in rivers occurs by choice of oviposition sites and is influenced by the evolved reproductive strategies of the individual species. Subsequent redistribution by migration or drifting establishes patterns which are then modified by environmental influences on growth and mortality. Continuity of life cycles is sustained by variations on a number of defined life history strategies combined with evolved behavioural responses.

### Introduction

A primary characteristic of all river systems is linear translocation of water and materials. All organisms living in rivers have to utilise or withstand such conditions. Superimposed on the translocational element are strong cyclical variations in factors such as discharge, temperature and illumination. Secondary to these physical cycles are interactive seasonal changes in plant growth and in sediment deposition and erosion. Life history strategies are thought to have been moulded by natural selection to exploit these fluctuations in the environment. For instance, seasonal variations in a specific resource may be utilised either by organisms with short life cycles and extended resting stages or by longer lived forms capable of switching resources in times of scarcity.

Invertebrate distributions are determined in the first instance by oviposition or by drifting and settlement of the aquatic stages. Distributions thus initiated can be subsequently modified by redistribution through drifting or active migration.

Environmental cues for such migration include seasonal shifts in plant and sediment distributions. Competition, predation, disease and parasitism may affect behaviour so as to cause organisms to find new habitats as may physical and chemical stresses. Mortalities caused by these factors also alter distribution patterns.

Frid & Townsend (1989) list four criteria which should be considered when describing such mobile communities: (i) type of disturbance and the 'relict' community it leaves; (ii) factors influencing the supply of colonists; (iii) between patch variation; and (iv) the influence of first arrivals on subsequent colonisation. Unfortunately the full information on these aspects has never been available. However, in chalk streams, even though the associations of invertebrates are complex and diverse, sufficient is now known about the character of the streams and the stream fauna to permit conceptual modelling.

The present paper attempts to (i) provide information on the manner in which invertebrate distribution patterns are initiated; (ii) discuss how such distributions are subsequently modified; and

(iii) explore how shifts in distribution can be related to known life histories. Obviously all these aspects are intimately interrelated.

MacArthur & Wilson (1967) first drew attention to the apparently limited number of sets of life history strategies seen in extant organisms, i.e. many traits appear to act as covariables. Their explanation of this phenomenon was r- k- selection theory which was further expanded by Pianka (1970). However, this theory was strongly criticised for being too deterministic (Stearns, 1977) and has now been superseded by more stochastic models. A general theory to explain the limited set of life history strategies has not yet been forthcoming but there is broad agreement about the central role of trade-offs between life cycle variables in life history evolution (Sibly & Calow, 1983). An example of such a theory is the demographic theory of life history evolution (Tuomi *et al.*, 1983) which has three essential characteristics:

1. Natural selection acts on individual life history traits.
2. Natural selection optimizes adaptive strategies.
3. Individual life history traits are free to coevolve.

Most river invertebrates are relatively small compared to many terrestrial and marine taxa and, in the case of insects, most spend only the larval feeding stages in running water. Even the largest river dwelling species are only a few centimetres in length. Small size acts as a constraint on the reproductive strategies available to an organism. Since small size denies them very high levels of egg production, increased fecundity may most readily be achieved by increasing the number of broods produced over a period of time.

Within the river physical and chemical variables are characterised by longitudinal gradients and the fauna is often zoned accordingly along the length of the river at three levels.

1. Community zonation – with different functional groups often dominating the eroding and

sedimenting regions of the river system (Cummins, *et al.*, 1981).

2. Interspecific zonation – many families of insects, for example, show strongly developed patterns of species zonation (Ladle *et al.*, 1977).
3. Intraspecific zonation – life histories and growth patterns show systematic variation, within populations, along the length of streams (Fig. 1).

Within zones there are varying degrees of 'patchiness' in response to heterogeneity of physical factors. Differences in water velocity, turbulence, sediment type, light intensity etc. are associated with variation in food supply and induce differential growth and differential survival. How does this patchiness come into being? Patches can be created by uneven distribution of offspring which in turn depends on the reproductive tactics employed by the species in question. Invertebrate reproductive tactics can involve for example:

1. Eggs laid in sites selected by adults (e.g. Simuliidae)
2. Eggs laid where adults live and feed (e.g. Oligochaeta)
3. Eggs brooded by adults after eclosion (e.g. Amphipoda, Sphaeriidae).

### Initiation of distributions

Species which do not brood the eggs have a wide choice of situations in which eclosion can occur. Some fully aquatic forms such as snails oviposit on the surfaces of stones or plants where the young will be able to graze soon after hatching without the need to undertake a hazardous migration from oviposition to feeding sites. However the eggs of such species are potentially vulnerable to predation and are often enclosed in tough gelatinous coatings for protection. Some insects also oviposit beneath the water surface. The small caddis fly *Brachycentrus subnubilus* Curtis emerges over a short period in April–May and the eggs are laid in great gelatinous masses on the underside of floating marginal grasses or debris (Gunn, 1985).

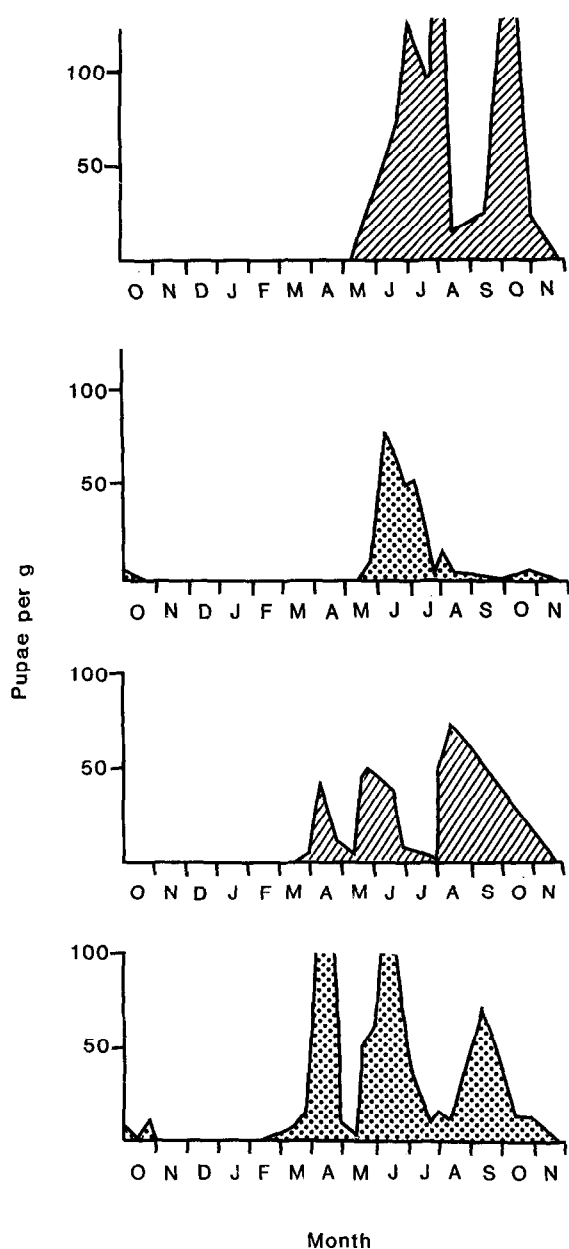


Fig. 1. Patterns of density (numbers  $\text{g}^{-1}$  of dried *Ranunculus*) of pupae of *Simulium equinum* (lines) and of *Simulium lineatum* (dots) at sites separated by 4 km on the River Frome, Dorset. Each major peak represents the culmination of a generation.

One of the best examples of site selection by insects is seen in the Simuliidae. The larvae of this family are passive suspension feeders (dependent on the flowing water to supply their food), show few morphological differences between species

and are often extremely abundant. Consequently it is likely that there will be a strong element of interspecific competition for food and feeding sites. In fact spatial segregation of species is often well marked and the individual species are in many cases restricted to particular zones of the river system (Ladle *et al.*, 1977). Feeding site selection is by a combination of oviposition site choice and subsequent readjustment by drifting.

Ovipositing female *Simulium equinum* L. place the eggs on trailing vegetation, at or just beneath the water surface (Welton & Bass, 1980) and such sites are most abundant on small narrow streams. The closely related species *Simulium lineatum* Meigen oviposits while resting on the water surface in situations with smooth, more or less laminar flow and proportionately greater areas of suitable conditions occur in broader, downstream reaches. The distribution of *S. equinum* extends into more turbulent tributaries while that of *S. lineatum* does not.

There is also a temporal element involved in species zonation. Simuliidae in chalk streams are mostly multivoltine and each generation may inhabit a different zone of the river (Ladle *et al.*, 1977). A few specialised forms which inhabit winterbournes (*Metacnephia amphora* Ladle & Bass) or riffles downstream of impounded sections of river (*Simulium posticum* Meigen) have only a single annual generation and in these oviposition behaviour places the eggs in the dry bed or banks of the river (Ladle *et al.*, 1985). Complex diapauses prior to hatching ensure that the subsequent eclosion does not occur when conditions are adverse to survival of the larvae. In the case of *S. posticum*, a man-biting pest (Hansford & Ladle, 1979), the larvae show little temporal overlap with sympatric species of Simuliidae, a feature which permits the possibility of specific control measures applied in the 'time window' when only the target species is vulnerable.

Oligochaeta of at least four families are present in abundance in chalk-stream habitats. Sexual reproduction in most species is by the production of cocoons containing a (small) number of fertilised eggs. The Tubificidae which mostly inhabit soft sediments of sand and silt tend to reproduce

sexually in winter and early spring. The Naididae, in contrast, generally alternate between sexual and asexual reproduction. The latter predominates during periods of rapid population increase under conditions of low stable flow, high water temperatures and abundant food supply within the algal associations on the surface of macrophytes and river bed stones (Ladle, 1971). Under appropriate conditions an asexually reproducing individual could produce twice as many offspring as an equivalent sexually reproducing form. The Lumbriculidae, containing rather few species, includes one, *Lumbriculus variegatus* (Müller), which rarely if ever reproduces by sexual means. The Enchytraeidae are predominantly a terrestrial group with some members which live in stream bed sediments (Johnson, 1989). Perhaps surprisingly in view of their small size many Enchytraeidae are very slow to grow and reproduce in aquatic situations. Reproduction is normally by sexual production of cocoons at relatively long intervals of time and each containing only a very small number of eggs, a strategy which may possibly relate to their survival in ephemeral stream habitats where they are often found.

In flowing water situations several fully aquatic species from a wide range of taxonomic groups have evolved breeding strategies which involve brooding and care of the young. In leeches, amphipods, isopods, sphaeriid bivalves and gastropods systems have developed by means of which the juvenile stages can be protected and supported for considerable periods of time. Since the young animals are carried about with the parent until release there are limitations on the number of young in each brood. *Gammarus pulex* (L.) females may carry up to forty eggs in the brood pouch, the numbers increasing with increasing size of female (Welton, 1979). The animals breed throughout the year in chalk streams but the greatest mean size and consequently the largest broods occur in May and June. Brood development times are also less at higher water temperatures (Welton & Clarke, 1980) and in its lifetime a female *Gammarus* may produce six broods. The highest population densities of *Gammarus* are normally found in association with aquatic mac-

rophytes such as *Callitriche* or *Ranunculus*. The highest densities of juveniles are found in the shelter of macrophytes in late summer and early autumn, a situation into which they are released by the females. Juvenile *Gammarus* still in the brood pouch may feed actively on fine particles of detritus brought to them in the respiratory current of the female. After release they feed predominantly on fine material deposited within the shelter of macrophytes including faecal material from the adults.

Sphaeriids are also abundant in chalk-stream sediments and some species such as *Pisidium subtruncatum* Malm, *P. milium* Held and *P. nitidum* Jenyns are almost ubiquitous (Ham & Bass, 1982). As in *Gammarus* litter size increases with the body size of the parent (the organisms are hermaphrodite). At the time of release the young are about 25% of the parental length and, in chalk streams, broods are released in June and October (Ladle & Baron, 1969) and high densities of young occur in the finely particulate marginal sediments inhabited by the adults.

### Redistribution

Having established the basic distributions through selection of oviposition (reproduction) sites all species undergo rearrangement by various degrees of active or passive translocation. Physical and biological phenomena in rivers follow a number of cyclic annual changes which influence invertebrate distributions. Essentially, the winter increase in flow causes extensive erosion and redeposition of fine sediments. The growth of diatoms on gravel and plant surfaces in April is the first phase of primary production and is soon followed by rapid increase of submerged macrophytes which trap and stabilise extensive deposits of fine inorganic and organic sediment. Subsequent encroachment of marginal plants increases the accumulation of sediment, particularly fine highly-organic silts, and shades out or smothers the growths of rheophilous macrophytes.

The annual increase in flow flushes out shal-

lowly rooted plants and at the same time sorts and redistributes much of the fine sediment. Virtually all chalk stream invertebrates are intimately associated with plants or sediments and must either tolerate or accommodate to the sequence of changes described.

Passive, often catastrophic, drift is associated with flooding and the attendant increases in water levels, velocities and turbulence. River bed sediments are swept into suspension and redeposited, together with many of the burrowing organisms, in other areas. During such events it is probable that there is a certain amount of sorting related to the physical (settlement) characteristics of the organisms concerned.

The simplest form of redistribution is passive scattering along with the eroding sediments in autumn and winter. Some Tubificidae, such as *Tubifex tubifex* (Müller) and *Limnodrilus hoffmeisteri* Claparède, mainly inhabit the superficial fine deposits and since they are unable to swim actively they are swept along by the flow and deposited with the lower density fractions of silt and organic matter (Fig. 2). Breeding and cocoon production in these species takes place in late winter following the main period of washout and enables rapid recolonisation of the habitat generated following the high flows by the offspring of the redistributed adults (Ladle, 1971).

Following eclosion some species drift from the egg laying sites to positions more suitable for feeding. First instar simuliids, for example, produce a silk thread which acts as a form of parachute and anchor line. After drifting downstream the thread adheres to plant surfaces and the larva creeps down and attaches by means of a silk pad to its feeding station. Some lotic Chironomidae may drift in the first or second instars before settling into their 'preferred' habitats (Storey, 1986). Similar behaviour patterns are probably widespread in other groups.

When invertebrates become large enough to migrate actively or drift selectively they may then make choices of habitat. Such choices will be influenced by factors such as availability of food, intra- and interspecific interactions and innate responses to physical and chemical characteristics

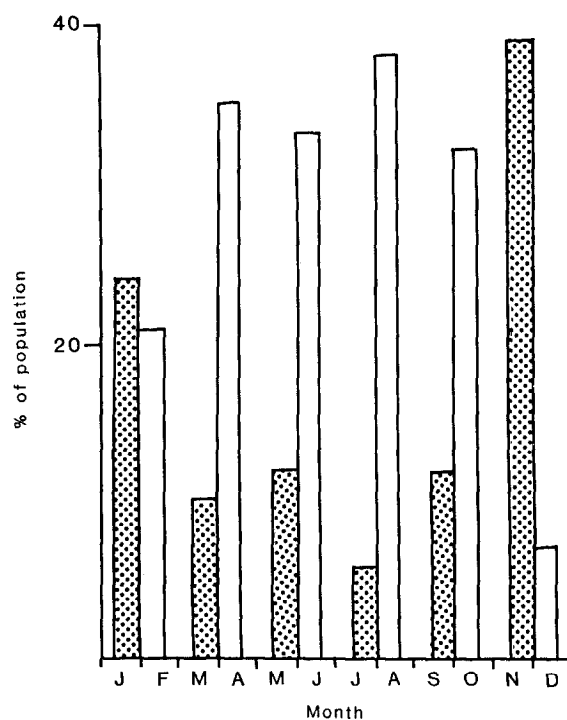


Fig. 2. Seasonal redistribution of oligochaete associations following winter increases in flow in a stream bed, gravel habitat. Open columns represent oligochaete species associated with gravel substrata and shaded columns species which are characteristic of silty substrata.

within the river environment. Most, if not all, species probably adjust their primary distributions to a greater or lesser degree. Litterick (1973) suggests that 'upstream migration played a significant part in the recovery of *Gammarus pulex*' following displacement by catastrophic flows in a small chalk stream. He also showed that upstream migration may be restricted to particular size categories of *Gammarus*. Adams *et al.* (1987), studying the same species, demonstrated that larger animals are associated with larger substratum particles and that in a uniform substratum of smaller particles the animals tend to move upstream.

### Patchiness

Having selected or attained their habitats in a variable ecosystem the patchily distributed invertebrates are subject to factors which will induce

local differences in population density, feeding rate and growth. These are interactive with variations in food supply and other ecological variables. For example slow flow has been found to be associated with the attainment of large body size in chironomids (Welton *et al.*, 1987). The interpretation of these phenomena is rendered more complex by the relationship between population density and size in some chironomids which may become cannibalistic at high population densities (McLachlan, 1989).

Results of studies in experimental stream channels (Ladle & Welton, 1984; Ladle *et al.*, 1984, Ladle *et al.*, 1985b) have demonstrated that chironomids may respond to differences in physical conditions by alterations in both population density and/or growth and size (factors which are themselves interactive). There is no reason to suppose that other invertebrates do not react in a similar fashion. It is certain that, within the complex mosaic of stream-bed habitats, species distributions will exhibit spatial variation of, not only population density (intensity), but also feeding rates, growth rates and definitive sizes attained.

Rosillon (1988) showed experimentally that growth responses of *Ephemerella ignita* (Poda) to water temperature variations differed according to the quality of the available food for that species. In natural streams there is considerable variation in the quality of food from place to place and between the microhabitats occupied by individual animals. Thorough understanding and modelling of such variation could provide the most appropriate tool for management and conservation of rivers.

### Continuity

Having considered in some detail the potential variations of life cycles in relation to habitat selection and responses to a variable environment the remaining question is – How do river invertebrates sustain continuity of life cycles? Or, ‘Where do the flies go in the wintertime (summertime)?’ The answers appear to be represented in four different strategies –

1. They have a continuous series of generations with adaptations of each generation appropriate to maintenance of continuity. Overwintering larvae developing at low temperatures, for example, produce relatively large adults which compensate for high winter mortalities by the production of more eggs. In this instance each generation may be considered as a different entity with a specific group of adaptations to cope with a rapidly changing environment.
2. They have a long life of one or more years. This is generally associated with relatively large size and ultimately with high levels of egg production. In this case selection pressures on the juvenile stages must be relatively low.
3. They have a short life span followed by a long resting stage which spans periods of adverse conditions such as drying of the stream or winter weather. Resting stages often involve subtle selection of resting sites and/or adaptations to resist physical damage or to avoid predation hazards.
4. They have an alternation of sexual and asexual phases with the latter often occurring in periods of stability and abundant resources and the former taking place at the onset of deteriorating conditions.

Other strategies are possible and variations or combinations of the four common types mentioned above provide the basis of a wide spectrum of possible life cycles. Superimposed on these broad life history strategies are the behavioural and physiological responses to short term changes and seasonally repeated environmental events. Such responses are themselves subject to selective pressures and as such provide the inbuilt flexibility and resilience needed to accommodate life histories to the vagaries of a spatially and temporally variable environment.

### Conclusion

In conclusion it would appear that the many life history strategies encountered in chalk streams do not easily conform to any unified theory. However, Tuomi *et al.* (1983) present a demographic

theory of which the essentials require that (i) natural selection should operate on specific life history traits; (ii) that, in this way, adaptive strategies should be optimised; and (iii) that individual life history traits should be free to coevolve, none of which seem to be inconsistent with the examples and principles presented.

## References

- Adams, J., J. Gee, P. Greenwood, S. McKelvey & R. Perry, 1987. Factors affecting the microdistribution of *Gammarus pulex* (Amphipoda): an experimental study. *Freshwat. Biol.* 17: 307–316.
- Cummins, K. W., M. J. Klug, G. M. Ward, G. L. Spengler, R. W. Speaker, R. W. Ovink, D. C. Mahan & R. C. Petersen, 1981. Trends in particulate organic matter fluxes, community processes and macroinvertebrate functional groups along a Great Lakes Drainage Basin river continuum. *Verh. int. Ver. Limnol.* 21: 841–850.
- Frid, C. L. J. & C. R. Townsend, 1989. An appraisal of the patch dynamics concept in stream and marine benthic communities whose members are highly mobile. *Oikos* 56: 1.
- Gunn, R. J. M., 1985. The biology of *Brachycentrus subnubilus* Curtis (Trichoptera) in the River Frome, Dorset. *Hydrobiologia* 120: 133–140.
- Ham, S. F. & J. A. B. Bass, 1982. The distribution of Sphaeriidae in rivers and streams of central southern England. *J. Conch.* 31: 45–55.
- Hansford, R. G. & M. Ladle, 1979. The medical importance and behaviour of *Simulium austeni* Edwards (Diptera Simuliidae) in England. *Bull. ent. Res.* 69: 33–41.
- Johnson, P. & M. Ladle, 1989. The Enchytraeidae (Oligochaeta) of streams of southern England. *Ann. Limnol.* 25: 121–129.
- Ladle, M., 1971. The biology of Oligochaeta from Dorset chalk streams. *Freshwat. Biol.* 1: 83–97.
- Ladle, M. & F. Baron, 1969. Studies on three species of *Pisidium* (Mollusca: Bivalvia) from a chalk stream. *J. anim. Ecol.* 38: 407–413.
- Ladle, M. & J. A. B. Bass, 1975. A new species of *Metacnephia* Crosskey (Diptera: Simuliidae) from the south of England, with notes on its habitat and biology. *Hydrobiologia* 47: 193–207.
- Ladle, M., J. A. B. Bass & L. J. Cannicott, 1985. A unique strategy of blackfly oviposition (Diptera: Simuliidae). *Entomologist's Gaz.* 36: 147–149.
- Ladle, M., J. A. B. Bass, F. R. Philpott & A. Jeffery, 1977. Observations on the ecology of Simuliidae from the River Frome, Dorset. *Ecol. Entomology* 2: 197–204.
- Ladle, M. & G. J. Bird, 1980. Aquatic Oligochaeta of southern England. In R. O. Brinkhurst & D. G. Cook (eds), *Aquatic Oligochaete Biology*. 165–174.
- Ladle, M., D. A. Cooling, J. S. Welton & J. A. B. Bass, 1985b. Studies on Chironomidae in experimental recirculating stream systems. II. The growth, development and production of a spring generation of *Orthocladius* (*Euorthocladius*) *calvus* sp. nov. *Freshwat. Biol.* 15: 243–255.
- Ladle, M. & J. S. Welton, 1984. The ecology of chalkstream invertebrates studied in a recirculating stream. *Ann. Rep. Freshwat. Biol. Ass.* 52: 63–74.
- Ladle, M., J. S. Welton & J. A. B. Bass, 1984. Larval growth and production of three species of Chironomidae from an experimental recirculating stream. *Arch. Hydrobiol.* 102: 201–214.
- Litterick, M. R., 1973. The drifting and upstream movement of the macro-invertebrate fauna of a chalk stream. PhD thesis, University of Hull, 136 pp.
- MacArthur, R. H. & E. O. Wilson (1987) *The theory of island biogeography*. Princetown University Press, Princetown, New Jersey.
- MacLachlan, A. J. (1989) *Animal populations of extreme densities: size dimorphism by frequency dependent selection in ephemeral habitats*. *Funct. Ecol.* 3: 633–643.
- Pianka, E. R., 1970. On r- and k- selection. *Am. Nat.* 104: 592–597.
- Rosillon, D., 1988. Food preference and relative influence of temperature and food quality on life history characteristics of a grazing mayfly, *Ephemerella ignita* (Poda). *Can. J. Zool.* 66: 1474–1481.
- Stearns, S. C. (1977) *The evolution of life history traits*. *Ann. Rev. Ecol. Syst.* 8: 145–171.
- Storey, A. W., 1986. Population dynamics, production and ecology of three species of epiphytic chironomid. PhD thesis, University of Reading, 342 pp.
- Tuomi, J., T. Hakala & E. Haukioja, 1983. Alternative concepts of reproductive effort, costs of reproduction, and selection in life history evolution. *Am. Zool.* 23: 25–34.
- Welton, J. S., 1979. Life-history and production of the amphipod *Gammarus pulex* in a Dorset chalk stream. *Freshwat. Biol.* 9: 263–275.
- Welton, J. S. & J. A. B. Bass, 1980. Quantitative studies on the eggs of *Simulium* (*Simulium*) *ornatum* Meigen and *Simulium* (*Wilhelmia*) *equinum* L. in a chalk stream in southern England. *Ecol. Entomology* 5: 87–96.
- Welton, J. S., J. A. B. Bass, M. Ladle & W. J. Merrett, 1987. Distribution of oviposition sites and characteristics of egg development in the 'Blandford Fly' *Simulium posticum* (Diptera: Simuliidae). *J. appl. Ecol.* 24: 865–879.
- Welton, J. S. & R. T. Clarke, 1980. Laboratory studies on the reproduction and growth of the amphipod *Gammarus pulex*. *J. anim. Ecol.* 49: 581–592.