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# THE POPULATION BIOLOGY OF *Crenobia alpina* (Dana)

A thesis submitted to the University of Glasgow
for the degree of Doctor of Philosophy
in the Faculty of Science

by

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July 1983

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# SUMMARY

An investigation was carried out into the relationship between environment and reproduction in the freshwater triclad species *C.alpina*. By studying two populations occupying adjacent habitats, under varying conditions of temperature, flow rate and resource availability, the effects of habitat variability on the distribution, density, size structure and the levels of sexual and asexual reproduction within each population were assessed. The population occupying a habitat which was characterised by its eurythermic temperature regime, high flow rates and complex macroinvertebrate community, occurred at low densities. Within this population, individuals were larger, on average, than in the adjacent population, and sexual reproduction occurred at high levels throughout the year, with asexual reproduction (by binary and multiple fission) also occurring throughout the year, but at lower levels. The seasonal nature of this habitat was reflected within the population of *C.alpina*, which exhibited spring peaks in density, followed by summer peaks in the level of sexual reproduction.

In contrast, the adjacent population occupied a habitat which was characterised by its stenothermic temperature regime, low flow rates and a less complex macroinvertebrate community, and occurred at much higher densities. Within this population, individuals were smaller, on average, than in the adjacent population, and sexual reproduction was virtually absent, with asexual

reproduction (by binary and multiple fission) occurring throughout the year at appreciable levels. The lack of seasonality within this habitat was similarly reflected in the lack of any seasonal fluctuations in density, or level of (in this case asexual) reproduction within the population. The level of food availability varied seasonally in both habitats, however, and was generally similar, in terms of biomass, in both areas.

A hypothesis was presented which related the density of triclads within each habitat to the total food availability, measured as stream drift. It was suggested that at low population densities, the relatively higher levels of net resource availability per individual favoured the occurrence of sexual reproduction, in contrast with situations of high population density, where the relatively lower levels of net resource availability per individual inhibited the occurrence of sexual reproduction, thus favouring asexual reproduction.

This hypothesis was supported by the results of laboratory investigations in other studies, together with the evidence gained from field observations from this study, particularly the observation that in the low density population, seasonal cycles in the level of sexual reproduction were out of phase with seasonal cycles of a similar nature in the level of population density.

Further evidence, from the results of a field manipulation experiment, was presented which supported the hypothesis. In an area of high population density, density was reduced artificially, resulting in a significant increase in the level of sexual reproduction within the population. It was concluded that in the high density population, intense intraspecific competition for food resulted in a low net level of food availability per individual, which in turn inhibited the process of sexualisation in triclads from that area.

The results from these two populations of C.alpina, indicating that net food availability controls the occurrence of sexual reproduction in this species, are in marked contrast to the findings of previous studies, in which habitat temperature is implicated as the dominant environmental influence on this process.

We split the difference and the ripples magnified,
Learning, looking under stones,
To find the worm disturbed - he turns and turns,
We always were the curious kind...

(Jeanette Obstoj, 1982)

# CHAPTER ONE

# INTRODUCTION

In a paper published in the American Naturalist in 1932, H.J.Muller stated categorically that "genetics has finally solved the age-old problem of sexuality and sex...". That this statement was premature is evident when it is noted that in 1973, G.C.Williams referred to the aforementioned problem as a "crisis... in evolutionary biology". Of all the questions which arise out of the theory of evolution by natural selection as proposed by Darwin (1859), the question "why sex?" has proved among the most intractable.

In the Animal Kingdom, the process of reproduction is manifold and ubiquitous. Despite the complexities, however, it is possible to distinguish between two fundamentally different reproductive patterns.

The first of these patterns is referred to as asexual reproduction. In asexual reproduction, new individuals or offspring are produced as a result of mitotic activity usually referred to either as budding or gemmation (Abercrombie et al. 1981). This may be of a simple form as found in Protozoa, in which the division of one parent (or cell) results in the production of two daughter organisms. In Metazoa, however, the process is slightly more complicated, since the production of new organisms involves the coordinated action of certain localised groups of cells which bud off to form a new individual. Asexual reproduction, therefore, involves the use of a cellular process of controlled mitoses. By definition this precludes the generation of genetic diversity through the actions of meiosis and recombination.

Sexual reproduction, which is by far the more common method of producing offspring, is based fundamentally on meiosis and involves not only controlled mitotic proliferation of cells during the growth of progeny, but also, and more importantly, an initial cell fusion (zygote formation) before this period of growth can occur (the exception being parthenogenesis- see below). The formation of the zygote at syngamy results in the mixing of genetic material from both parents, forming a genetically 'new' individual. In the case of parthenogenesis, the genetic material present in the offspring is entirely derived from and identical to the maternal genome, the role of the male gamete being either merely a developmental trigger as in automixis, or entirely absent as in apomixis.

Sex is also characteristically associated with the possession by the parent of specific cell types, normally found grouped into gonadal tissue (either ovary or testis). Other related reproductive strucures which, together with gonads, form the 'reproductive system' are also normally present e.g. copulatory apparatus and egg-packaging system, although the function of some of these may be redundant in parthenogenetic species. It is important to note that there has been an overwhelming tendency in scientific literature to classify parthenogenesis as 'asexual' reproduction. I consider this to be mistaken both for reasons quoted above, and also for reasons which will be considered later. Any reference made to asexual organisms during the course of this thesis, therefore, shall exclude parthenogenetic organisms, since

|  | AMEIOTIC | MEIOTIC |
|---|---|---|
| GAMETIC | PARTHENOGENESIS (APOMIXIS) | PARTHENOGENESIS (AUTOMIXIS)<br>SYNGAMY |
| NON-GAMETIC | FISSION / GEMMATION |  |

Table 1: Classification of animal reproduction
- for an explanation see text.

I consider parthenogenesis to be an extreme variant of sexual reproduction. A summary of these definitions is given in Table 1.

In order to explain why sexual reproduction is so common, it has been necessary to split the question into two parts i.e. why is sexuality more successful than asexuality as a long term evolutionary strategy (i.e. over many generations)? And, why is sexuality more successful than asexuality as a short term evolutionary strategy (i.e. from generation to generation)? The former question has largely been answered in theoretical terms by Williams (1975) and Maynard Smith (1978), by assuming that asexual lines (both include parthenogenetic lines in this category), being genetically static, are unable to adapt to an environment which alters through time e.g. through climatic changes, whereas sexual lines, by virtue of their ability to generate new assortments of characters, are better able to 'track' such changes, and hence persist in the environment for longer periods. Difficulties have arisen in trying to explain the advantages of sex as a short term evolutionary strategy, however, since this involves the sexual organism having to gain sufficient selective advantage within a single generation over asexual competitors, which often possess potentially higher rates of population increase. In producing theoretical models in attempt to explain this situation, Williams (1975) and Maynard Smith (1978) have considered the ability of a sexual group to overcome a 'twofold cost of meiosis' (the cost of producing males) which is not incurred by a competing group of conspecific self-replicating females (i.e. parthenogenetic organisms - asexual by their definition). In order that the sexual group may out-compete the 'asexual' group, the following two assumptions must hold:

(i) Strong selection pressures must operate from one generation to the next.

(ii) The 'asexual' group must consist of a very limited number of genotypes (normally one or two).

Considering the nature of intraspecific competition, assumption (i) is probably valid, and assumption (ii) is consistent with what is known about the genetics of parthenogenetic animals (but see Suomalainen and Saura (1973) for an alternative view on this), but the question arises: Does the model tackle the problem of competition between sexual and asexual groups, or is it merely an examination of competition between two divergent sexual types? I believe the latter to be the case for the following reason: Parthenogenetic gametes are produced by the same systems which produce sexual gametes, asexual propagules (e.g. fission fragments) are produced by different systems. In a comparison of sexual with parthenogenetic reproduction, it is valid to consider how sex 'overcomes the twofold cost of meiosis' not incurred in parthenogenesis, since the two processes differ only in this respect, and are otherwise fundamentally the same. Asexual reproduction (my definition - see Table 1) differs fundamentally from sexual reproduction in many respects other than merely the absence of meiosis, therefore to compare the two processes only in terms of this single, though important difference is misleading. I therefore consider that the question: 'Why is sexuality more successful than asexuality as a short term evolutionary strategy?' remains as yet unanswered. I believe the difficulties involved in identifying the short term advantages of sex arise mainly from the poorly described nature of asexual reproduction, a point I shall return to in Chapter 4.

The evolutionary ecology of asexually reproducing populations has received scant attention in the literature, with a few notable exceptions (Shick and Lamb 1977; Calow et al. 1979; Beveridge 1981). Having noted this, it is not surprising that the phenomenon of asexual reproduction is so poorly understood.

If an answer to the question of the short term advantage of sex is to be found, then a good area to start would be the study of populations which exhibit both sexual and asexual reproduction. Indeed, this point has been stressed by Calow et al. (1979). One of the species which they suggest for consideration is the stream-dwelling triclad *Crenobia alpina* (Dana), the species on which this study was carried out.

As a group, the freshwater triclads have proved of great value in substantiating and redefining many areas of ecological theory e.g. work on competition between lake-dwelling species by Reynoldson (for refs. see Ball and Reynoldson 1981) and on the theory of feeding strategies in multispecies assemblages (Calow et al. 1981; Adams 1980a, 1980b). Of particular relevance to this study, however, are the studies of Calow and co-workers (for refs. see Calow et al. 1981) on life-history strategies. This work centres on the reproductive responses of a number of different species to varying environmental constraints, especially temperature and resource availability. Although the major part of this work has been carried out on purely sexual species, more recently Calow et al. (1979) have considered the relative costs and benefits of asexual reproduction within the strictly asexual (in the British Isles) species Polycelis felina (Dalyell). A natural continuation of this line of research has been to consider what environmental constraints are operating to control reproduction within a species-population which exhibits both sexual and asexual reproduction. This forms the linking theme of the work contained in this thesis.

The species C.alpina is one of three species of freshwater triclad found in the British Isles which is known to reproduce both sexually and asexually (Ball and Reynoldson 1981). In the following chapters I shall consider how key environmental factors influence the life cycle of this species, with special emphasis being placed on reproduction.

The results of field observations and experiments on a selected species-population of C.alpina form the major part of this thesis, and are presented in Chapter 3. The major aim of the work described in this chapter was to attempt to understand the environmental conditions within the habitat of an organism (in this case C.alpina) which influence the relative occurrence of sexual and asexual reproduction. The population of C.alpina chosen proved ideal for these purposes, for a number of reasons: Firstly, it was known to include both sexually and asexually reproducing individuals. Secondly, and more importantly, it became obvious, following an initial period of sampling, that the study population could be divided into two discrete sub-populations, occupying different areas of the study locale. A clear difference in the pattern of reproduction within each sub-population was the criterion used: In one sub-population (occupying what was referred to as the 'downstream' area), sexual reproduction was common, in the other (occupying what was referred to as the 'upstream' area), sexual reproduction was scarce, almost to the point of non-occurrence. It was considered that an investigation of the possible causes of such a radical difference between two adjacent populations could shed much light on the factors in the environment which were controlling the occurrence of sexual reproduction. With this aim in mind, the field work decribed in Chapter 3 followed two major lines of investigation, decribed separately in Sections A and B: The results presented in Section A seek to illustrate the differences existing between the habitats occupied by each population. This was achieved by monitoring abiotic environmental factors such as temperature and flow conditions, and biotic factors such as resource availability, together with a consideration of the macroinvertebrate community structure of each area. In Section B, the population biology of C.alpina within each habitat is considered, with particular emphasis being placed on obtaining more detailed information on reproduction. Information is presented on such factors as population density and potential causes of mortality, together with a consideration of the influence of reproductive differences on the population size structure at the two areas. In the final section of Chapter 3, the differences existing between the habitats occupied by each population presented in Section A is considered in relation to the demographic differences outlined in Section B. In particular, the relationship between population density, resource availability and the occurrence and level of sexual reproduction within each population is discussed, together with the wider implications of the results presented on these populations to the species C.alpina as a whole. Finally, a hypothesis is presented which attempts to explain the results of the field study; this hypothesis is tested experimentally, and the results obtained are discussed, together with suggestions for further research in this area.

Finally, in Chapter 4, I return to the argument described earlier in this chapter concerning the natures of sexual and asexual reproduction, discussing the results obtained here, together with those from other studies in relation to current theories concerning triclad life-cycle strategies. I also consider the problem from an evolutionary standpoint, extending the argument to include other animal groups.

# CHAPTER TWO

# LITERATURE REVIEW

## (i):Introduction

The stream-dwelling triclad species of the British Isles and continental Europe have been the subjects of many studies by freshwater biologists over the past two centuries. Consequently, a considerable amount is known about their biology, particularly in relation to the problems of taxonomy and geographical distribution. Of the species of freshwater triclad found in Europe which commonly inhabit lotic (i.e.flowing water) systems, three are found in the British Isles:

Polycelis felina (Dalyell 1814)
Crenobia alpina (Dana 1766)
Phagocata vitta (Duges 1766)

The existence of such a vast amount of literature precludes a comprehensive review relating to all species. I therefore concentrate, in this chapter, on the literature dealing specifically with C.alpina. I consider other work, where relevant, in the succeeding chapters.

## (ii):Taxonomy

The species now recognised as Crenobia alpina was first described by Dana in 1766 as Hirudo alpina. It was soon renamed by Linnaeus in 1768 to incorporate it into his genus Fasciola, which included both parasitic and free living flatworms. After subsequently reverting to Hirudo alpina three years later, the species underwent a variety of name changes (some due to misidentification, others to spelling errors), a fact which illustrates the extremely confused nature of flatworm taxonomy during that period.

| | |
|---|---|
| *Hirudo alpina n.sp.* | : Dana (1766). |
| *Fasciola alpina* | : Linnaeus (1768). |
| *Hirudo alpina n.sp.* | : Rozier (1771) (reference in Kenk(1974)) |
| *Planaria arethusa n.sp* | : Dalyell (1814). |
| *Planaria alpina* | : Kennel (1888). |
| *Crenobia alpina* | : Kenk (1930)-IN CURRENT USAGE |

TABLE 2 : A LIST OF THE VARIOUS TAXONOMIC NAMES OF THE SPECIES Crenobia alpina (Dana).

In 1888, Kennel placed the species in the genus *Planaria* (created by Muller in 1776) where it remained until 1930, when Kenk, in his taxonomic review of the Probursalia, created the genus *Crenobia* to describe the species, finally naming it *Crenobia alpina* (for refs. see Kenk 1974). The various taxonomic names of *Crenobia alpina* are listed together with sources in Table 2.

The genus *Crenobia* is characterised by the distinctive structure of its atrial muscle plates (Ball and Reynoldson 1981). The only monopharyngeal representative of the genus, *C.alpina* occurs as a number of varieties found in groundwater and lotic systems throughout Europe (ibid.). The existence of these varieties is undoubtedly a major cause of the confusion and misidentification of the species in the literature. Another factor in this is that earlier descriptions of the species were based solely on morphological characteristics, which are known to be unreliable; e.g. variation in the size of the head tentacles is more likely to be phenotypic, rather than genetic, in origin (Dahm 1958). However, a number of authorities have considered the existence of these varieties to be worthy of further investigation (Thienemann 1938,1950; Dahm 1958), and I shall consider their views in the following section, in relation to the zoogeography of the species in Europe.

### (iii): Zoogeography and the Existence of Races

By far the greater part of the research carried out in Europe on C.alpina has been concerned with its zoogeography, particularly in relation to the distribution of varieties or "races" described by Thienemann (1950). Consequently, a great deal is known of the distribution of the species throughout Europe.

C.alpina has a wide, if discontinuous pattern of distribution in Europe. Its range extends from the Faroe Islands and Fennoscandia in the north (Ullyott 1935; Dahm 1958) to the Mediterranean island of Corsica in the south (Benazzi 1961), and from Poland (Dudziak 1956) across central Europe to the British Isles. It is absent, however, from the Iberian peninsula (Dahm and Gourbault 1978) although present in the Pyrenees (Dahm 1958). Within these areas, C.alpina is typically found in upland cool running water habitats such as mountain streams and the upper reaches of rivers, although its distribution ranges down to sea-level in some areas (Ball and Reynoldson 1981). It is also, though less commonly, found in two types of lentic habitat: the littoral regions of high altitude / latitude lakes (Reynoldson 1953; Ball and Reynoldson 1981), and the deep sublittoral of alpine lakes (Schmassman 1920, in Dahm 1958). However, evidence has recently been obtained (Baird and Beveridge in prep.), which raises doubts as to the permanence of littoral lake-dwelling populations.

Concerning the existence of races, Thienemann (1950) concluded from a critical study of observations by previous authors, that the following five forms of *C.alpina* occurred :

*C.alpina meridionalis*
— two main types
*C.alpina septentrionalis*
*C.alpina var. alba* – a Belgian form
*C.alpina var. corsica* – a Corsican form
*C.alpina var. bathycola* – a deep alpine lake form

He believed that the forms *C.alpina meridionalis* and *C.alpina septentrionalis* constituted two recognisably distinct types within the 'type species' *C.alpina typica*; to the other forms he assigned the category 'varieties'. Thienemann distinguished between the two main types as follows: *C.alpina meridionalis* was generally darkly pigmented, with a southerly distribution centering on Middle Germany and the Alps, and reproduced sexually all year round. *C.alpina septentrionalis*, on the other hand, was lightly pigmented, with a more northerly distribution extending into Scandinavia, and reproduced almost exclusively asexually by fission. He also cited differences in the structure of the gut diverticulae and chromosome number as existing between the two types.

The discrete nature of the distribution patterns of the two types became somewhat blurred following Dahm's (1958) reappraisal of the situation. He sampled *C.alpina* from a wide number of localities throughout Europe, and found that Thienemann's two types (in relation to mode of reproduction) could be further extended to three types, by addition of a type which reproduced equally commonly by both sexual and asexual means. These three types conformed to no rigorously separable distribution pattern, except that the most northerly populations tended to conform to Thienemann's description of C.alpina septentrionalis However, Dahm (1958) explicitly considered the karyotype of the various populations studied, and provided evidence for the existence, not only of a certain degree of karyotypic variability, but also of an incidence of polyploidy which suggests that multiplication of the genome is the norm in this species. This lack of conservatism in karyotype can commonly lead to the production of aneuploid gametes, which in turn effectively blocks meiosis and hence inhibits sexual reproduction (White 1973).

Dahm's study, therefore, is an explanation for the existence of C.alpina septentrionalis types (i.e.those which reproduce strictly asexually): asexual populations may appear randomly, presumably persisting in favourable habitats. These randomly arising populations, while all conforming to strict asexuality, may not necessarily be more closely related genetically to each other than to neighbouring populations of the other two types. It would be spurious, therefore, to assign asexual populations to the C.alpina septentrionalis 'type' merely on the criterion of mode of reproduction. The fact that more northerly populations tend to be of the C.alpina septentrionalis 'type', therefore, may only reflect the fact that more northerly habitats are in general more favourable to asexuality, and not necessarily that all populations arose from the same genetic stock.

At the present time, it is impossible to assess the validity of Thienemann's claims until further work is carried out along the lines of Dahm's (1958) study, particularly work of a karyological nature. Until then , the status of these 'types' remains doubtful.

Both the geographic distribution of this species, and its classification as a stenotherm (a point which I shall consider later) have led to it being described as a 'glacial relict species' (Voigt 1892,1904 - refs. in Wright 1968) which has recolonised Europe from its preglacial centre of distribution, the Alps (Thienemann 1950). Other workers (Ullyott 1936; Dahm 1958, Wright 1968) have concurred with this view, although de Beaufort (1951) is a notable exception. His criticism centres around Ekman's (1915) description of a glacial relict species:

(i) The species should be a cold-water stenotherm.
(ii) Its dispersal mechanisms should be restricted
(iii) It should have lived in its present locality since glacial times, evidenced by a fossil record.

As Wright (1968) has stated, condition (iii) is almost impossible to prove, since C.alpina has no fossil record, recent or otherwise. However, de Beaufort (1951) claimed that Lauterborn's (1921) report of C.alpina in N.Africa and Arndt's (1922) report of the species in Corsica, suggest that its distribution does not conform to that expected of a glacial relict. However, it seems likely that Lauterborn was incorrect in his report (see Thienemann 1938) and consequently de Beaufort's argument collapses.

Indeed, the debate as to whether or not *C.alpina* is a glacial relict species becomes largely academic, when one realises, as Wright (1968) did, that the real problem lies in the lack of agreement over the true definition of a glacial relict species.

## (iv): Distribution in the British Isles

Despite the fact that *C.alpina* is found throughout the British Isles in a variety of habitats, no comprehensive distribution maps are currently available, although one is in preparation (Bellamy, pers.comm.). The most recent summary of its distribution is given by Wright (1968) in which he provides a map illustrating the reports of *C.alpina* available in he literature up to that date

Early records of *C.alpina* in lotic systems date back to Dalyell (1815,1853) who describes the existence of populations of *Planaria arethusa* (later identified as *C.alpina* - see Kenk 1974) in springs at Foulden, Berwickshire, and at Binns, Linlithgowshire. Later records from Scotland include Whitehead 1922, Dahm 1958, Morgan and Egglishaw 1965, and Maitland 1966. The species has also been recorded from other areas in the British Isles (refs. in Wright 1968) particularly in Wales (e.g. Carpenter 1928; Reynoldson 1956; Wright 1968,1972,1974; Lock and Reynoldson 1976) although records from southern and eastern areas of England are less common (e.g. Beauchamp and Ullyott 1932; Burkill 1957; Ball 1967). *C.alpina* has also been recorded from Ireland (Southern

1936) although its distribution there is largely unknown. The picture which emerges from the available data, therefore, is one of a species which is evenly distributed in the north and west of Great Britain, becoming more sporadically distributed in the south and east. This chiefly reflects the availability of suitable habitats for C.alpina (i.e.upland springs and stream systems), which are more sparse in southern and eastern areas (Wright 1968).

C.alpina has also been recorded from the littoral regions of some northern lochs (Reynoldson 1953,1958; Reynoldson et al. 1981; IUCN, pers.comm), although there remains some doubt as to whether or not these records indicate that C.alpina is a permanent member of the littoral community (Baird and Beveridge in prep.)

## (v):Factors Influencing Local Distribution and Abundance

Despite considerable amounts of research carried out on this subject, there still remains a great deal of doubt as to which environmental factors are of the greatest importance in limiting the local distribution and abundance of C.alpina i.e. its presence within particular freshwater habitats.

These factors fall into two basic categories: those which I shall refer to as abiotic factors, chiefly temperature and flow rate; and biotic factors, the major components in this case being food availability and competition (these being inextricably linked in most studies).

It is now generally accepted that temperature is one of the most important factors influencing the life cycle of freshwater triclads (Dahm 1958; Pattee et al. 1973; Calow 1977). That it is a key factor in influencing the distribution and abundance of *C.alpina* is also similarly accepted. However there is still some doubt as to the nature of its influence on the life cycle. The major area of doubt concerns the relationship between temperature and mode of reproduction; this being greatly complicated by the vast and generally conflicting amounts of data available on the subject. The influence of temperature on reproduction is of central importance to this study, and shall be considered in detail later, for the moment I shall consider more general aspects.

*C.alpina* is generally referred to in the literature as a stenotherm (Steinmann 1907; Carpenter 1928; Beauchamp 1932,1933,1935,1937; Schlieper and Blasing 1952,1953; Pattee et al. 1973). However there is some doubt as to whether this description has any real meaning. Precht et al. (1973) state:

> 'The expressions stenothermal and eurythermal have not yet been precisely defined. A species may be called eurythermal if it occurs in regions with greatly differing temperatures; but it still must be shown that it does not consist of genetically distinct stenothermal races. Furthermore, a species may be given the name if it tolerates large seasonal temperature fluctuations, a phenomenon that may be influenced by temperature-independent factors or by special resting phases. Finally, the ability to endure temperature changes during one season must be considered. Genetic adaptations will be found oftener (sic.) in stenothermal species or races, non-genetic ones in eurytherms.'

It is in the nature of its wide distribution that studies on C.alpina have tended to show a lack of agreement on the upper and lower limits of its thermal tolerance. Attempts to make comparisons of these measures between such widely differing climatic regions as Eastern Europe (Dudziak 1956), the Alps (Thienemann 1950) and central France (Pattee 1966), or even between areas within the British Isles e.g. Wales (Carpenter 1928; Wright) 1968 and the Cotswolds (Beauchamp and Ullyott 1932; Burkill 1957) have led to increasing confusion concerning the true temperature 'preferences' of the species. Wright (1968) correctly sums up the problem :

> "It is probable that the relative importance of the factors forming the effective environment of a given species (of triclad) varies from one stream to another thus giving rise to conflicting views. Once identified, the relative importance of these factors for a given species must be assessed for each stream individually."

There seems little doubt, however, that where it occurs, C.alpina displays a marked preference for cool running water habitats. Kohler (1937) stated that C.alpina populations from middle Germany can tolerate temperatures of up to 14C, with an optimum around 0C. In the Cotswolds, Beauchamp and Ullyott (1932) found similarly that C.alpina was "more successful" (i.e. more abundant) at temperatures below 14C. Higher 'upper limit' figures abound in the literature (e.g.Carpenter 1928;Burkill 1957), and indeed Pattee (1965) has shown that high altitude populations in France can tolerate temperatures up to 25C in the daytime, but only if the temperature falls below 10C in the evenings.

Survivorship studies by Pattee et al. (1973) have demonstrated, again for French populations, that the upper limit for what he refers to as "infinite survival" is around 15C; lower limits of survival, they claim, are generally of less importance in limiting the distribution of this species, and this is true of triclads in general.

Owing to the wide interpopulation variation in measured thermal tolerance levels, and in the absence of a more comprehensive study of populations from a wide geographical range, it is therefore difficult to interpret data from previous studies in a meaningful way, particularly since nothing at all is known of the level of genetic similarity between any of the populations studied.

Direct physiological effects apart, temperature may also indirectly influence the distribution and abundance of C.alpina populations, particularly in relation to its influence on habitat productivity. Temperature is a constraint on the growth rates of all organisms (Calow and Townsend 1981) at all trophic levels within an ecosystem, and hence affects resource availability at each point in the food web. Temperature also influences oxygen saturation levels (see below).

Chemical factors, while often cited as limiting the distribution of C.alpina, on closer examination seem to be only of minor importance (Wright 1968).

Oxygen consumption in C.alpina is high relative to other triclad species (Whitney 1942), and indeed Blasing (1953) showed that a rise in temperature of 5C (from 5C -

10C) resulted in a sixfold increase in the rate of oxygen consumption. Flowing water habitats, with the exception of polluted habitats, normally exhibit high levels of oxygen saturation, and therefore it seems unlikely that *C.alpina* would be limited by oxygen availability in such situations. In lakes, however, this may not be the case, and Beauchamp (1932) suggests that the lower levels of oxygen saturation found in lake littoral habitats (relative to lotic systems) may be limiting to this species. It is also worth noting that *C.alpina* is markedly absent from polluted waters (Jones 1940; Van Oye 1950).

Bornhauser (1912) suggested that calcium and bicarbonate concentrations were limiting to *C.alpina* populations in his study. Records of the species from waters ranging from 0.5mg.Ca/litre (Carpenter 1928) to 123mg.Ca/litre (Wilhelmi 1923 *in* Wright 1968) suggest this claim to be without foundation. Similarly, Van Oye's (1950) observation that *C.alpina* existed in a limited pH range of 7.1-8.4 has not been confirmed elsewhere (c.f. Flossner 1959). Conclusive proof that *C.alpina* is tolerant of a wide range in pH and calcium/bicarbonate concentration has been provided by Wright (1968, 1974).

The response of *C.alpina* to current has normally been studied in comparison with other stream-dwelling triclad species in the laboratory (Pattee and Bournaud 1970; Lock 1972a,b,1975). In these studies, it was shown that *C.alpina* was more tolerant of high flow rates than other species considered. *C.alpina* could withstand currents of up to 34cm/s in the absence and up to 45cm/s in the presence of a stony substratum, compared with similarly obtained values for P.felina of 17cm/s and 21cm/s respectively (Lock 1972a). The difficulty of accurately simulating and measuring the effect of current flow in the laboratory are summarised in Lock (1972b). The results of these laboratory studies agree closely with field observations (Wright 1968, 1974) and have been of importance in assessing competitive interactions among stream-dwelling triclad species (see below).

First described by Voigt (1892, 1904 - refs in Wright, 1968), the competitive relationships between C.alpina and other stream-dwelling triclads have perhaps received more consideration than any other aspects of its biology. Despite this fact, however, some doubt still remains as to whether competition between C.alpina and other stream-dwelling triclad species (particularly P.felina in the British Isles) has been convincingly demonstrated.

Following Voigt's (1892, 1904) work, Beauchamp and Ullyott (1932) considered that solitary species within a stream were limited by the upper range in temperature of the habitat, whereas when two or more stream-dwelling species coexisted within a particular habitat, competition occurred, limiting the species concerned. Realising that temperature tolerance alone could not account for the competitive displacement of P.felina by C.alpina (few studies agreed on the temperature limits for C.alpina, Beauchamp and Ullyott (1932) invoked another factor, current flow, to explain the differences in distribution. Following this work, it has become generally accepted that both in continental Europe (Voigt 1892.,1904; Pattee 1966, 1969a, 1969b, 1980, Pattee et al. 1973) and in the British Isles (Carpenter 1928; Beauchamp and Ullyott 1932; Wright 1968,1972,1974,1975; Lock 1972a,b, 1975; Lock and Reynoldson 1976) competition does occur between these two species, although it has yet to be proven conclusively.

Reynoldson and Bellamy (1970) listed five criteria which collectively provide strong evidence for the existence of competitive interactions in a given situation: (i) the distribution/abundance of the two species should be consistent with a hypothesis of competition. (ii) It must be shown that intraspecific competition within the species-populations being studied is also occurring. (iii) Manipulation of both the common resource and the distribution/abundance of the two species should give results consistent with a competition hypothesis. (iv) Introduction or removal/reduction in the numbers of one of the species should give results (in relation to the other species) consistent with a competition hypothesis.

Criterion(i) has clearly been verified in the case of C.alpina, particularly by Wright (1974). The work of Lock and Reynoldson (1976) has demonstrated that (ii) is satisfied (the diets of both species overlap), and (iii) possibly occurs, but evidence presented for (iv), despite their conclusions, remains insufficiently convincing to finally prove the case for competition between these two species. In their evidence for (iv), they claim that in a habitat in which C.alpina and P.felina coexisted, with P. felina as the dominant species in terms of numbers, a crash in the numbers of P.felina resulted in a proportional increase in the numbers of C.alpina present. Although a large proportional change did occur, the actual absolute density of C.alpina does not increase to such a great extent, and in the absence of fully quantitative density estimates, any positive conclusions about competition between the two species in this case must be tentatively drawn..

Available data on the dietary requirements of C.alpina are few, but data provided by Wright (1968) suggested that the species fed largely on oligochaetes and arthropods, tending to ignore molluscs; these results were based on feeding experiments and gut squashes. Confirmation of the dietary preferences of C.alpina were provided by Lock (1972b) and Lock and Reynoldson (1976) who demonstrated, by serological techniques, that certain arthropods (Gammarus sp., Plecoptera and Trichoptera) were preferred to others (Ephemeroptera). No positive results for oligochaetes were obtained due to the poor reactivity of the anti-oligochaete antiserum. It is important to note, however, that apart from these two studies, little is known about the feeding ecology of this species, particularly concerning the limiting effects of food supply on the distribution and abundance of field populations.

A serological technique similar to the one mentioned above was used by Wright (1968, 1975) to study the effects of predation on populations of *C.alpina*. He identified four species which fed on *C.alpina*: one trichopteran larva (*Rhyacophila sp.*); and three plecopteran larvae (*Isoperla grammatica*, *Perlodes microcephala*, and *Dinocras cephalotes*). The last of these three plecopteran species,. *D.cephalotes* was found to limit the distribution of the species under some circumstances.

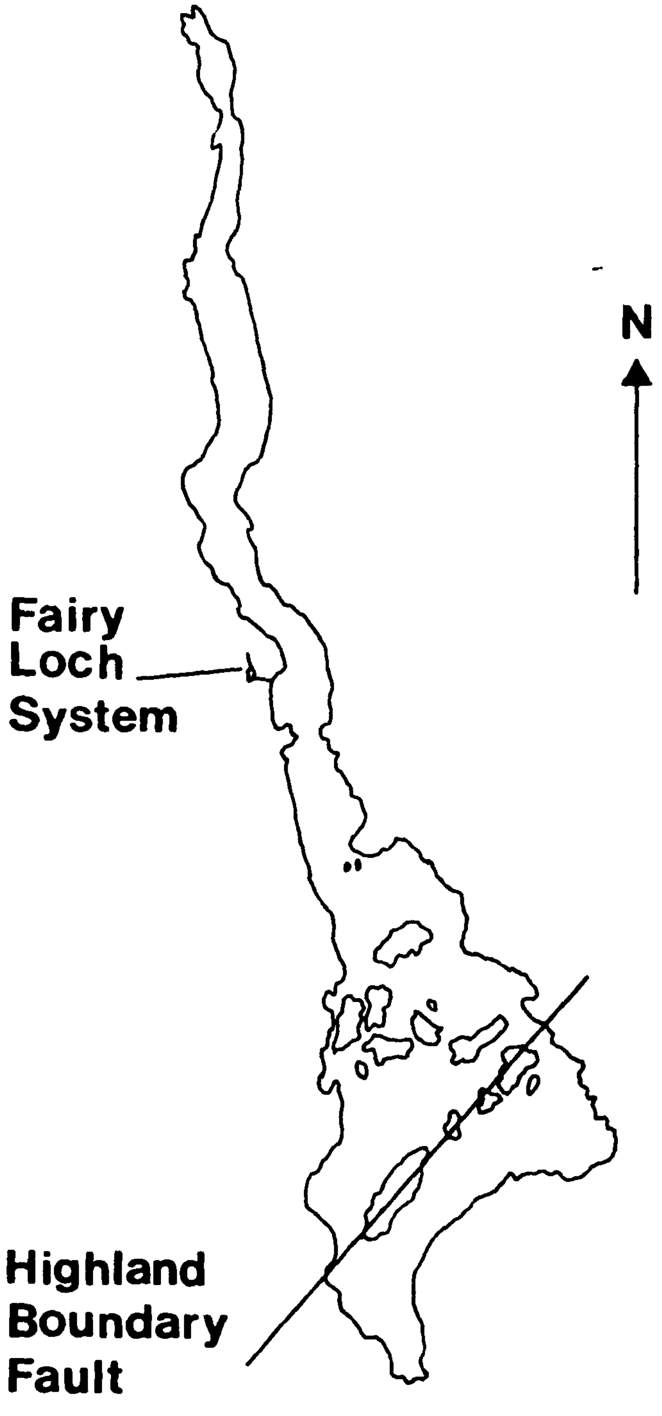
Wright (1968) and Lock (1972b) both note the occurrence of the facultative protozoan parasite *Tetrahymena pyriformis* in *C.alpina* populations, but neither considers it to be a possible limiting factor in the field. The opposite is certainly true for laboratory populations of *C.alpina*, to which this species constitutes a serious cause of mortality.

# CHAPTER THREE

# FIELD STUDY ON C.ALPINA

FIGURE 1

Sketch map of the Loch Lomond basin, showing the position of the study area, and the Highland Boundary Fault


N
Fairy
Loch
System
Highland
Boundary
Fault

## General Introduction

The results of the field study are presented here in two sections. The first section (A) deals with an analysis of the habitat occupied by the population of *Crenobia alpina* under study. The second section (B) is concerned with the dynamics of this population. In a third and final section, these results are discussed, and a hypothesis is presented which attempts to explain the results in section (B) in terms of those given in section (A).

## Section A : Analysis of the Habitat

### A(i) Introduction

This section presents information on both the abiotic and biotic components of the habitat occupied by the population of *C.alpina*. As mentioned in the previous chapter, all earlier field studies carried out on this species have shown the importance of obtaining detailed information of this kind, particularly when the life cycle of this species is under consideration.

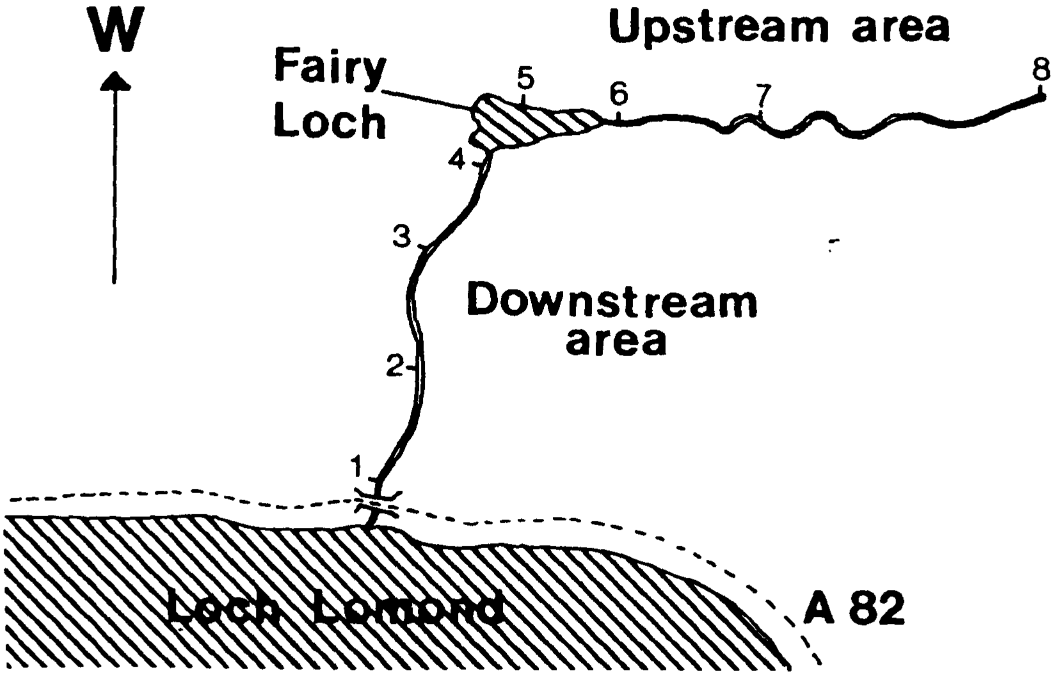
Following an initial five month period of preliminary investigation, a field sampling program was initiated from March 1980 on the basis of weekly visits to the study area. The position of the study site in relation to Loch Lomond is given in Figure 1. Eight sampling sites along the length of the habitat , separated by roughly equal distances, were chosen for intensive study (see Figure 2).

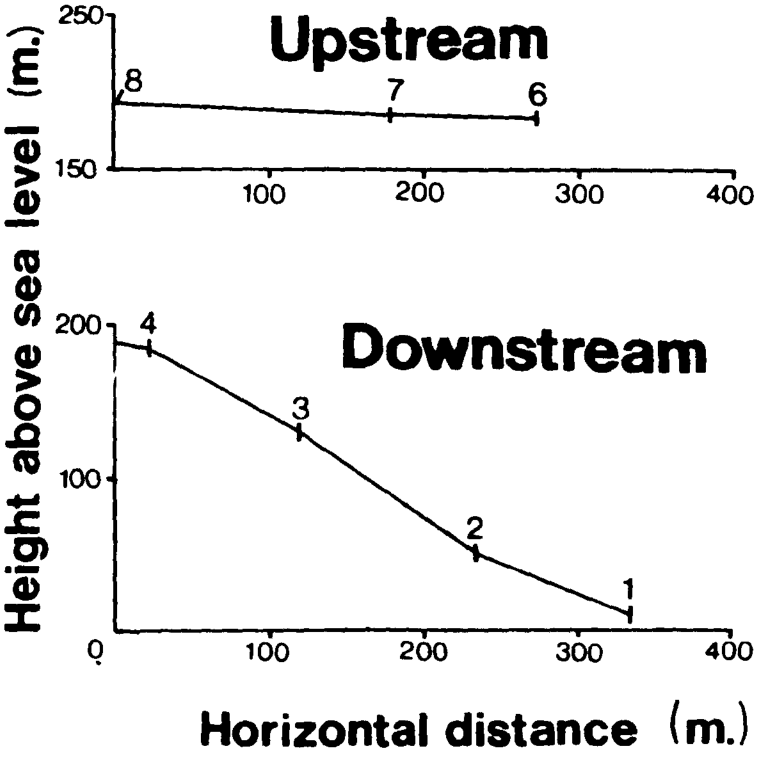
## FIGURE 2

Sketch map of the Fairy Loch System, showing the position of the sampling stations (1-8), and the 'upstream' and 'downstream' areas, in relation to the A82 road, and the shore of Loch Lomond.

## FIGURE 3

Gradient profile of the upstream and downstream areas.


W
Upstream area
Fairy Loch
5
6
7
8
4
3
2
1
Downstream area
Loch Lomond
A 82


Upstream
Downstream
Height above sea level (m.)
Horizontal distance (m.)
250
150
200
100
0
100
200
300
400
8
7
6
4
3
2
1

### A(ii) Topography and Site Description

Situated on the western shore of Loch Lomond (Grid Reference :NS339994), the study site was chosen primarily because it was the closest population of C.alpina which was known to contain both sexual and asexual triclads. A map showing its location is presented in Figure 2.

The study site itself can be divided into three discrete areas (see Fig. 2): a meandering stream averaging 1m wide by 0.1m deep, flowing from a helocrene source over an area of low gradient (see Fig. 3), fed by a number of very small springs along its length (this site will henceforth be referred to as the UPSTREAM area); this stream flows into a small mountain lochan which has become silted up and consolidated as sphagnum bog (designated on OS map NS39W (1:10000) as Lochan Uaine, but it is known locally as the FAIRY LOCH). The outflow from this loch is approximately 1.5m wide by 0.1m deep, flows down over an area of relatively steep gradient (see Fig. 3),and is culverted under the A82 road before flowing into Loch Lomond approximately 1.3Km north of Inverbeg.

In geological terms, the study area is situated on the western shore of a glacial valley, 15Km north of the Highland Boundary Fault which crosses Loch Lomond in a NE to SW direction from Balmaha on the eastern shore to Glen Fruin on the western shore (Slack 1957)-(see Fig. 1).

The stream system flows over an area of impermeable metamorphic rocks composed largely of mica-schists (Slack ibid.). This is of importance when considering the chemical properties of the water (see below).

The terrestrial vegetation surrounding the study area is typical of that found in the poorly drained slopes of the Loch Lomond basin. Bracken (*Pteridium aquilinum*) is the dominant terrestrial plant covering the land around the two stream areas; the Fairy Loch itself being covered by the bog moss (*Sphagnum palustre*). The sides of both stream areas are surrounded by trees, almost all of which are the birch *Betula pubescens*, although there are also oak (*Quercus petrea*), alder (*Alnus glutinosa*), hazel (*Corylus avellana*) and rowan (*Sorbus aucuparia*). These trees provide the major source of allochthonous resource input to the study system. The Fairy Loch itself possesses two other types of aquatic vegetation in addition to the bog moss i.e. the rush, *Eleocharis sp.*, and a species of *Potamogeton*. These, together with sparse clumps of the moss *Fontinalis*, present in the substratum of the upstream area, constitute the major source of autochthonous resource input to the study system.

### A(iii) Water Chemistry

#### Introduction

Analysis of the influence of chemical conditions on the distribution and abundance of *C.alpina* has produced much conflicting evidence (see Chapter 2). However, an analysis of a number of chemical constituents of the three study areas was carried out in order to assess possible differences between them, and also to obtain a better description of the study site as a whole.

| | Downstream | Upstream | L.Lomond |
|---|---|---|---|
| pH | 7.6 | 7.4 | 6.2 |
| Conductivity ($\Omega\ cm^{-1}$) | 77.3 | 84.1 | 44.9 |
| Alkalinity (meq.$l^{-1}$) | 1.05 | 1.03 | 0.98 |
| Dissolved Organic Matter (mg $O_2 l^{-1}$)<br>(measured as C.O.D.) | 0.64 | 0.87 | --- |
| Dissolved Oxygen (mg $l^{-1}$) | 13.0 | 12.2 | --- |
| Temperature (°C) | 5.6 | 6.2 | --- |

TABLE 3: Chemical analysis of water samples obtained from downstream (st.3) and upstream (st.6) areas, together with comparative data from Loch Lomond - samples collected 19.3.80.

## Methods

Water samples were collected in 1 l. polythene containers at stations 3 and 6, and returned to the laboratory for analysis. Oxygen saturation readings were taken in situ using a temperature/oxygen probe. In the laboratory, water samples were analysed for the following chemical constituents : pH, alkalinity, conductivity and dissolved organic matter (measured as C.O.D.). Both pH and conductivity were measured directly using chemical probes; alkalinity and dissolved organic matter were measured using water chemistry techniques modified from Mackereth et al.(1978) given in (U.F.S. Handbook, unpublished ms.) The samples were obtained on March 19th, 1980, together with a water sample from Loch Lomond (for comparative purposes).

## Results and Discussion

The results obtained are given in Table 3, and in general, are indicative of an unpolluted upland stream running over metamorphic rocks of the type described earlier. Both the downstream (st.3) and the upstream (st.6) areas are chemically rather similar, both had pH values higher than Loch Lomond, but were characterised by low concentrations of dissolved organic matter, indicating potentially low productivity in both areas. The conductivity of both samples from the study site is appreciably higher than that of Loch Lomond, indicating a higher ionic concentration of the water in those areas, but this is more likely to reflect the 'dilute' nature of Loch Lomond (Beveridge et al., unpub.report 1982) than any evidence of moderate levels of productivity in the streams, and this is confirmed by the extremely low alkalinity measurements. The levels of dissolved oxygen in both areas indicates almost 100% saturation, which again is typical of an unpolluted stream of moderate flow.

## A(iv) Temperatures

### Introduction and Methods

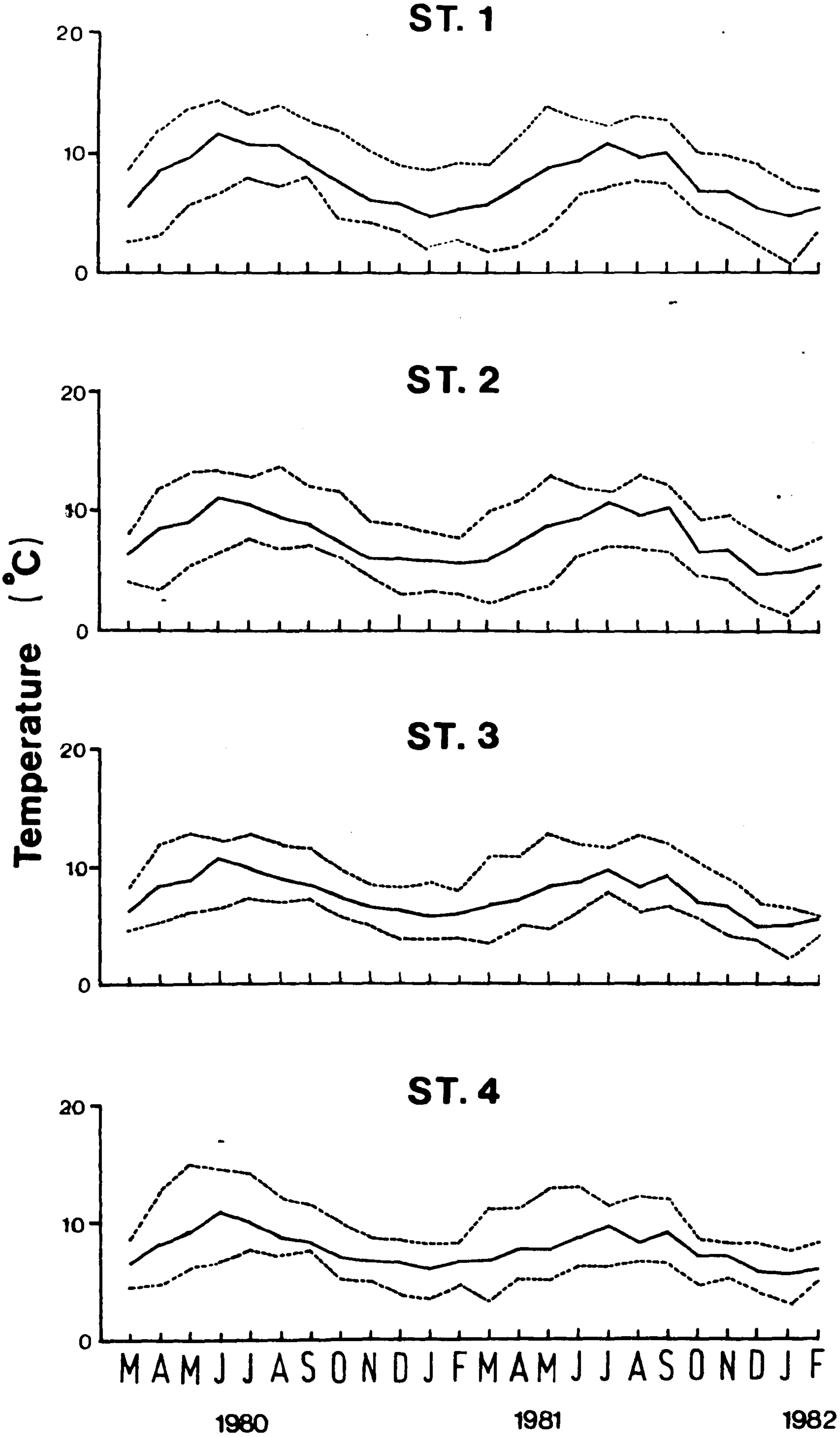
Temperature conditions on the eight stations chosen on the Fairy Loch system (see Fig. 2) were monitored on a weekly basis over the period March 1980 to February 1982. After consideration of a number of techniques, measurements were taken by regular inspection of maximum/minimum thermometers, coupled with simultaneous spot readings using a Digitron digital thermometer (model 4706). The maximum/minimum thermometers were calibrated, using the digital probe as standard, when necessary.

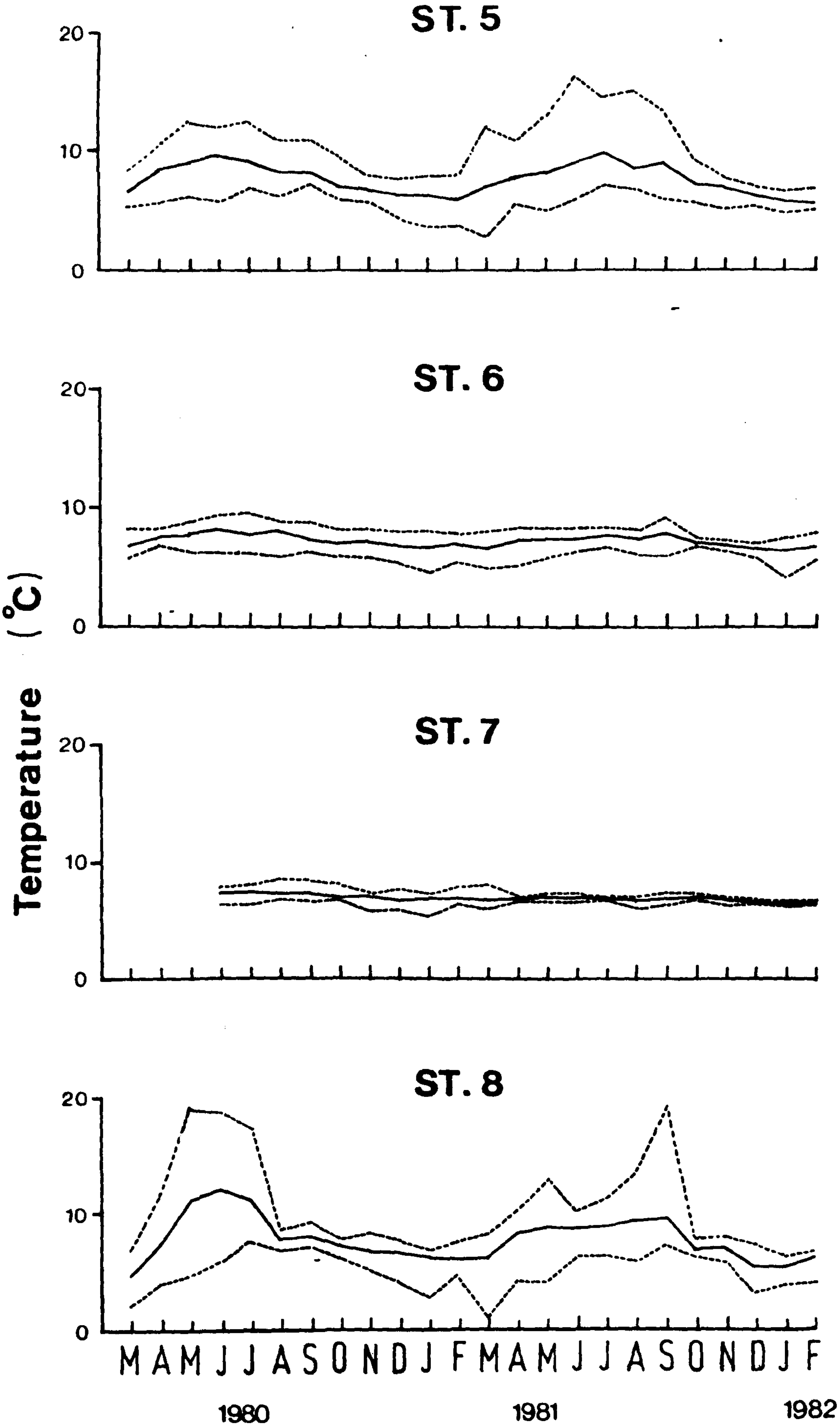
The placement of maximum/minimum thermometers in a highly turbulent environment, such as a mountain stream, poses problems concerning their protection from breakage. In this study, the thermometers were placed inside close fitting wire cages and anchored to the substratum. This provided protection from both breakage due to the downstream movement of the substratum (i.e. large boulders), and being washed away by the current. Despite these precautions, however, a number were lost, usually in conditions of extreme spate.

In order to minimise the effects of diurnal temperature fluctuations on the spot temperature readings, the data collected were obtained during the daytime period of 0930 to 1230 throughout the study. In order to avoid

## FIGURE 4

Maximum, minimum and spot temperature data for stations 1 - 8, collected over the period March 1980 to February 1982


ST. 1
ST. 2
ST. 3
ST. 4
Temperature (°C)
20
10
0
M A M J J A S O N D J F M A M J J A S O N D J F
1980
1981
1982

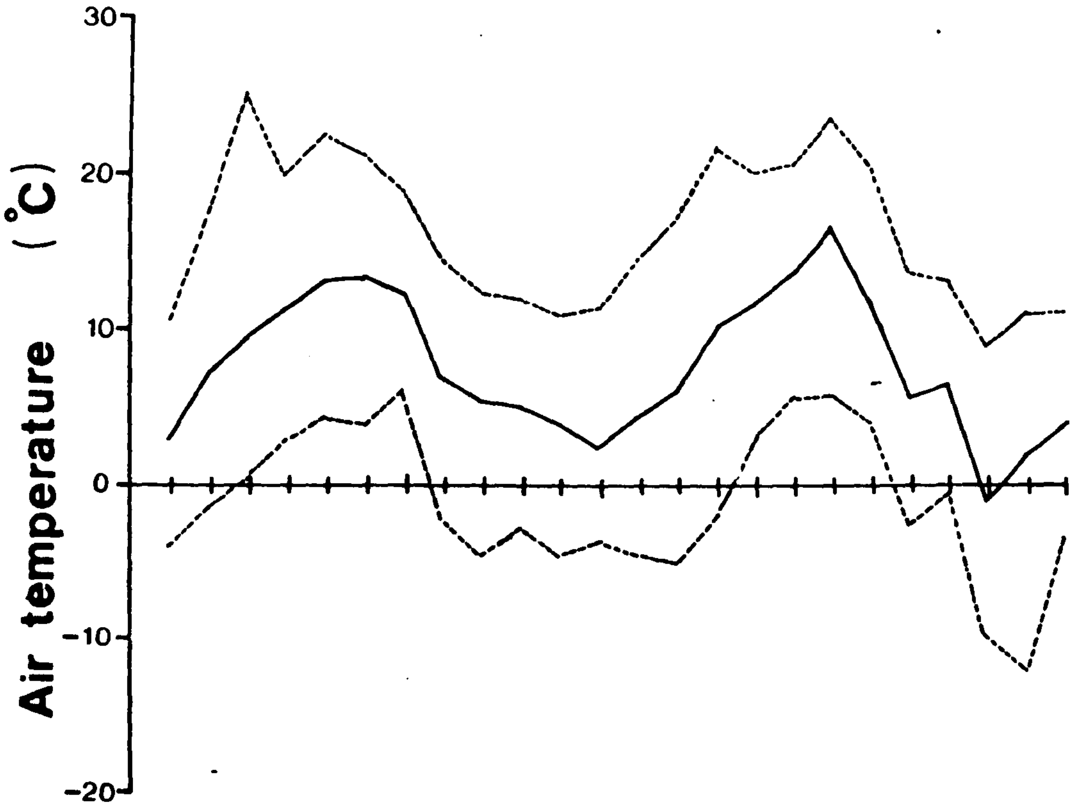

ST. 5
ST. 6
ST. 7
ST. 8
Temperature (°C)
20
10
0
M A M J J A S O N D J F M A M J J A S O N D J F
1980
1981
1982

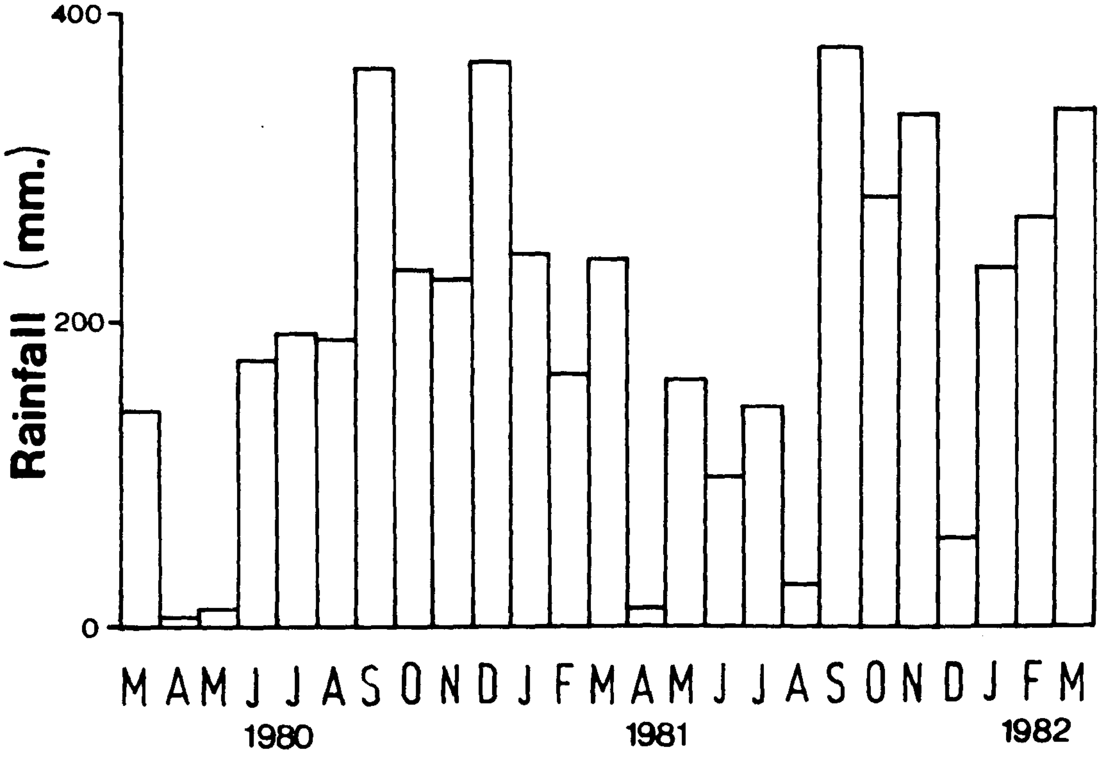
## FIGURE 5

Air temperature readings taken by the Clyde River Purification Board at Arrochymore, Loch Lomond, over the period March 1980 to February 1982

## FIGURE 6

Monthly rainfall totals collected by the Clyde River Purification Board at Inverbeg, Loch Lomond, over the period March 1980 to February 1982


Air temperature (°C)
30
20
10
0
-10
-20


Rainfall (mm.)
400
200
0
M A M J J A S O N D J F M A M J J A S O N D J F M
1980
1981
1982

the heating or cooling effects of exposure to ambient air temperature, the thermometers were read in situ, and were reset without removal from the water.

Data on local air temperature (readings taken at Arrochymore, Loch Lomond) collected by the Clyde River Purification Board are presented for comparative purposes.

## Results and Discussion

The temperatures obtained for stations 1-8 on the Fairy Loch system during the period March 1980 to February 1982 are presented in Figure 4. Air temperatures from the nearby station at Arrochymore for the same period are presented in Figure 5.

Data collected from the eight sites fall into two categories : Those which are 'seasonally uniform' (e.g. Fig.3, ST.6), and those which are 'seasonally variable' (e.g. Fig.3, ST.3). Data from stations 1,2,3,4 and 5 conform to the 'seasonally variable' type, which shall henceforth be referred to as the eurythermic pattern; stations 6 and 7 conform to the 'seasonally uniform' type, which shall henceforth be referred to as the stenothermic pattern. Data obtained for station 8 (the source) must be interpreted with caution, since for long periods of the year, the thermometer was not fully submerged (i.e. the source had all but dried up), and hence the readings reflected air temperature rather than water temperature.

Using temperature profile as a criterion, therefore, the Fairy Loch system can be viewed as two distinct regions. The downstream stations 1-4 show summer temperature maxima of 14.4C, 13.8C, 12.8C and 15.0C

| | ST.1 | ST.2 | ST.3 | ST.4 | ST.5 | ST.6 | ST.7 |
|---|---|---|---|---|---|---|---|
| SUMMER MAXIMUM | 14.4 | 13.8 | 12.8 | 15.0 | 16.0 | 9.6 | 8.4 |
| YEAR AND MONTHS ATTAINED | 6/1980 | 8/1980 | 5,7/1980<br>5,8/1981 | 5/1980 | 6/1981 | 7/1980 | 8,9/1981 |
| WINTER MINIMUM | 1.0 | 1.4 | 2.2 | 3.2 | 3.0 | 4.0 | 5.2 |
| YEAR AND MONTHS ATTAINED | 1/1982 | 1/1982 | 1/1982 | 1/1982 | 3/1981 | 1/1982 | 1/1981 |
| RANGE IN TEMPERATURE OVER 2 YEAR STUDY PERIOD | 13.4 | 12.4 | 10.6 | 11.8 | 13.0 | 5.6 | 3.2 |
| AVERAGE MONTHLY RANGE IN TEMPERATURE | 6.4 | 5.8 | 5.0 | 5.2 | 4.9 | 2.4 | 1.0 |

TABLE 4 :A summary of the temperature conditions prevailing throughout sampling stations 1-7 during the period March 1980-February 1981. (Data for st.8 not included - for reasons see text)

respectively, and winter temperature minima of 1.0C, 1.4C, 2.2C and 3.2C respectively. Station 5, the Fairy Loch itself, while not a strictly comparable habitat, exhibits a similar temperature regime to stations 1-4, with a summer maximum of 16.0C and a winter minimum of 3.0C. The upstream stations 6 and 7 provide a marked contrast, with summer maxima of 9.6C and 8.4C, and winter minima of 4.0C and 5.2C respectively. A summary of these data, together with between-station comparisons in temperature range is given in Table 4.

The explanation for these marked differences in temperature regime between stations 1-4 on the downstream area, which show strong seasonal variation, and stations 6 and 7 on the upstream area, which show little seasonal variation, is related to their respective catchment areas.

The upstream area, running parallel to a steep ridge along an area of shallow gradient receives its water input as runoff from the ridge, in the form of numerous small springs along its length. Since this water has percolated through the adjacent rock, by the time it emerges into the stream in the form of a spring, it has been appreciably cooled below air temperature. This water, typical of spring water, remains cool throughout the year, rendering the upstream area 'cool' in summer and 'warm' in winter, relative to air temperature.

The water input to the downstream system, however, flows directly out of the Fairy Loch itself, which is more strongly influenced by air temperature. Due to the lack of any similar springs along the length of the downstream area, the water temperature displays a similar temperature profile to that of its input supply.

These differences in water temperatures are important in their influence on biological processes such as metabolic rate, growth and hence production, and will be considered in the general discussion in section C of this Chapter.

## A(v) Flow Rates

### Introduction

Various authors (e.g. Beveridge 1981) have shown the importance of flow rate as a potential cause of mortality in stream-dwelling triclads. In a wider sense, however, flow rate has effects which are evident throughout lotic ecosystems, influencing the nature and amount of benthic production, the nature of the substratum, and therefore the structure and function of the existing community (Cummins and Klug 1980).

### Methods

The difficulty of obtaining accurate and biologically meaningful measurements of flow rate in field conditions has always hindered studies on the effects of current flow on field populations of stream-dwelling triclads. Ideally, current flow should be measured continuously, particularly in lotic systems subject to periodic spate conditions. Inability to do this, necessitating the substitution (for example) of weekly measurements, renders the data obtained of little value. Such data are further complicated by the necessity of placing the current probe in the same location every week. Even the slightest deviation from position may result in spurious readings, particularly in

|  | ST.1 | ST.2 | ST.3 | ST.4 | ST.6 | ST.7 | ST.8 |
|---|---|---|---|---|---|---|---|
| GRADIENT (%) | 40 | 67 | 46 | 25 | 2 | 4 | < 1 |
| RANK VALUE | 3 | 1 | 2 | 4 | 6 | 5 | 7 |
| 'CADDIS RATIO' | 2.5 | 14.7 | 4.8 | 1.2 | 0.5 | 0.7 | 0.1 |
| RANK VALUE | 3 | 1 | 2 | 4 | 6 | 5 | 7 |

TABLE 5: Indirect estimation of flow conditions: Gradient and caseless/cased caddis ratio data for stations 1,2,3,4,6,7 and 8, showing 100% agreement in ranked values.

streams with complex substrate (and hence complex flow) patterns. Wright (1968) suggests an alternative technique, involving measurement of gradient and rainfall. While the data generated by this technique are crude in comparison with direct measurement, they have certain advantages. By measuring the gradient difference, it is possible to rank sites according to increasing relative flow rate (assuming roughly constant gradient between sites) and by measuring rainfall, it is possible to assess the intensity of flow over the entire system throughout the year.

In addition, direct readings of flow rate were taken for the year 1981-1982 as part of the drift measurements for stations 3 and 6 (see later), and while these suffer from the problems outlined above, they are presented in Figure 13. Also, a biotic index of flow rate was calculated by comparing the abundance of trichopteran species in the ratio CASELESS CADDIS/CASED CADDIS. This ratio should increase directly with flow rate, according to the information given in Scott (1958), for similar species groups, and has been calculated from absolute (pooled) numbers of each group collected over the period March 1980 to February 1981 in monthly invertebrate samples (see later in this section), and is presented for comparative purposes.

## Results and Discussion

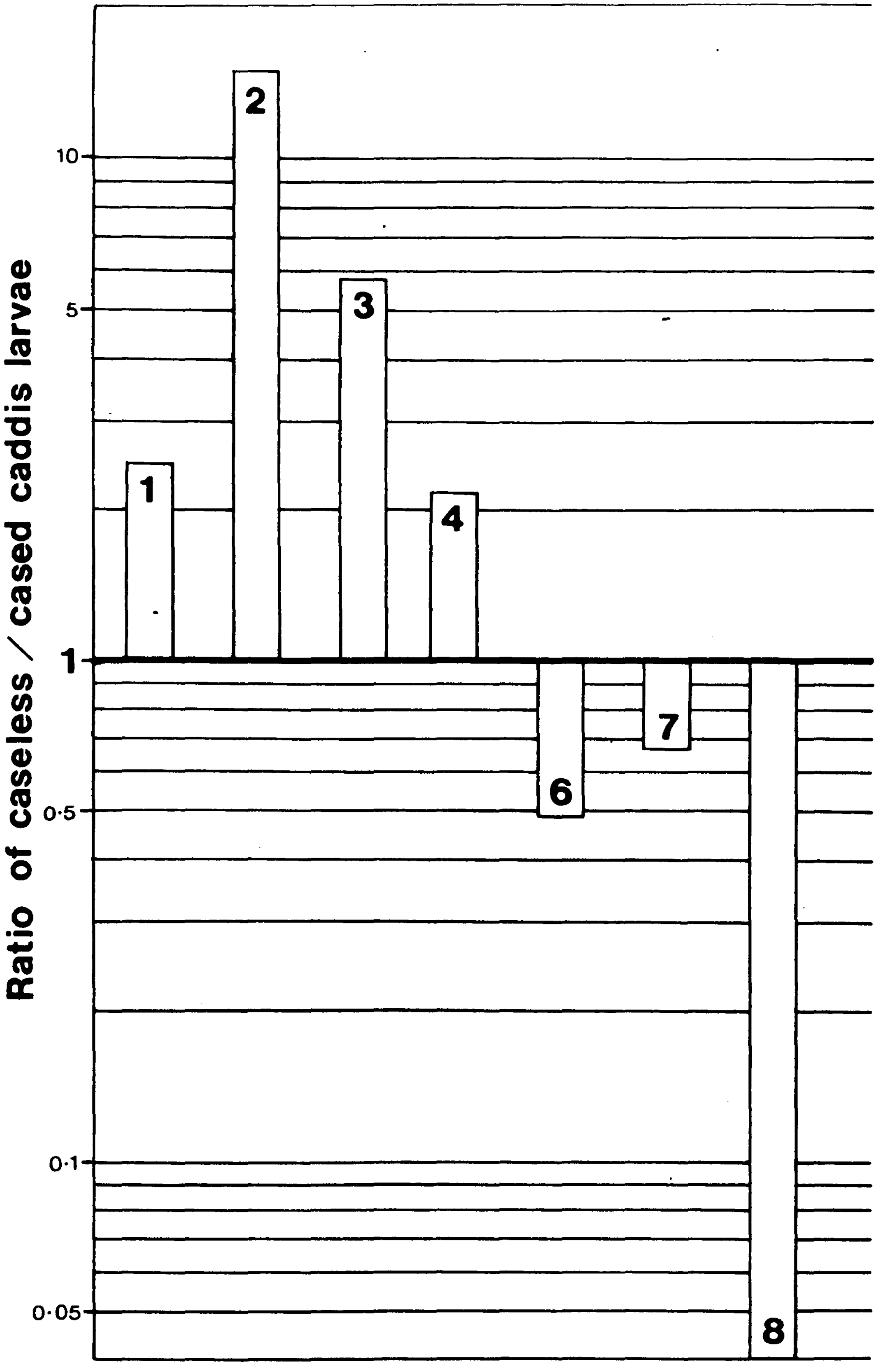
Gradient was measured directly from Ordnance Survey map NS 39 W (scale 1:10000) for each sampling station (station 5 was excluded, being a strictly lentic area). Data obtained are presented and ranked in Table 5.

| 1980 | RAINFALL (mm) | 1981 | RAINFALL (mm) | 1982 | RAINFALL (mm) |
|---|---|---|---|---|---|
| | | January | 244.8 | January | 235.9 |
| | | February | 166.4 | February | 268.0 |
| March | 142.8 | March | 240.9 | March | 339.5 |
| April | 7.7 | April | 11.6 | | |
| May | 12.9 | May | 162.0 | | |
| June | 175.8 | June | 99.0 | | |
| July | 192.9 | July | 144.6 | | |
| August | 188.9 | August | 28.6 | | |
| September | 362.8 | September | 377.2 | | |
| October | 234.5 | October | 281.5 | | |
| November | 228.8 | November | 335.8 | | |
| December | 367.6 | December | 57.4 | | |

TABLE 6: Monthly rainfall totals at Arrochymore, Loch Lomond, collected by the Clyde River Purification Board over the period March 1980 to March 1982.

FIGURE 7

Ratio of caseless / cased caddis from pooled monthly kick sample data at stations 1,2,3,4,6,7 and 8.


Ratio of caseless / cased caddis larvae
10
5
1
0·5
0·1
0·05
1
2
3
4
6
7
8

Rainfall data were obtained from the nearby Clyde River Purification Board station at Inverbeg (grid ref. NS 344981) and are presented as monthly totals covering the period March 1980 to March 1982 in Table 6. A graph comparing the flow rate between stations 3 and 6 (together with associated rainfall totals) over the period April 1981 to March 1982 is given in Figure 13. Table 5 also lists the ratio of caseless / cased caddis for stations 1,2,3,4,6,7 and 8, and these data are summarised in Figure 7.

## Discussion

There seems little doubt that the major differences in flow rate existing between the two areas relates to their respective topographies. This is reflected in the gradient values given in Table 5. The upstream area is typified by the meandering nature of its course; the substratum alternating between areas of pebble and gravel with a partial cover of *Fontinalis* and areas of dark brown silt. The downstream area, however, follows a much straighter course, with little or no cover of macrophytes, and no corresponding areas of silt. The upstream area, therefore, is characterised by its depositional nature, whereas the downstream area is markedly an erosional system.

If a direct relationship is assumed between the level of precipitation and the intensity of flow, then the precipitation pattern shown in the data for Inverbeg (Table 6; Fig.6) would predict that the periods of maximum flow rate are during autumn / early winter (i.e. September to February). This pattern may be complicated, however, by periods of low temperature over the winter months, when precipitation may be in the form of snow. This may result in the precipitation remaining 'locked up' for considerable periods, thus introducing a delay factor, until it melts in the warmer temperatures of early spring. This was certainly true for the winter of 1981/1982 during the latter stages of the study period, although it presumably had less effect in the milder winter of 1980/1981. It should be noted, however, that at no time did ice form on the streams in the upstream or downstream areas during the study period.

If the flow regimes of the two study areas shown in Figure 13 are examined, it can be seen that at both stations sampled (downstream st.3; upstream st.6) the period of maximum flow rates occurred during the months of September to November. This agrees well with the periods of maximum precipitation (shown for this period also in Fig.13). A subsequent decrease in flow rates over the winter months at both stations, despite relatively high precipitation values, relates to the 'lag' mentioned above. This corresponded with extremely low air temperatures which reflected one of the severest winters on record. Taking this factor into account, the relationship between precipitation and flow rate at these two stations is a close one, thus lending validity to the assumption made earlier. If these data for stations 3 and 6 are examined comparatively, it can be seen that in late spring and summer, the flow regimes are roughly similar, whereas in autumn and winter they diverge markedly. The downstream station (3), as predicted, had a much higher overall flow regime (maximum recorded flow = 1.58 $ms^{-1}$ ) than the upstream station (6) (maximum recorded flow = 0.88 $ms^{-1}$ ).

Finally, if the 'caddis ratios' are examined, it is clear that the rankings resulting from these data correspond completely to those calculated for gradient at each station.

The overall conclusion that can be drawn from this section, therefore, is that the upstream area possesses a flow regime of a much lower order than the downstream area, as a direct consequence of the differences in topography between the two areas. This difference in flow regime becomes increasingly marked during periods of high precipitation (i.e. during the months September to March). These differences may have important implications for the triclad population, and the community structure of both areas. These are considered in later sections of this chapter.

## A(vi) Community Structure

### Introduction

The major aim of this section is to analyse and comment on the macroinvertebrate species composition at the sampling stations chosen along the study area. Qualitative, rather than quantitative information was desired, in order to make broad predictions concerning functional aspects of the community, particularly where these had a potentially direct effect on the C.alpina population being studied.

The structure of stream communities is shaped by a variety of physical and biological factors, such as current flow, substratum and the nature of primary resource input (Hynes 1970; Boling et al. 1975; Cummins and Klug 1980). It must be borne in mind, however, particularly in the light of recent findings (Reice 1980), that the structure of lotic communities is extremely loose, both in space (due to the high mobility of the fauna) and in time (due to the relative unpredictability of running water habitats). 'Spot' measurements of community structure, while providing information which may be useful in a predictive sense (such as the 'caddis ratio' presented earlier in this section), must be considered with caution. This is particularly important, since the study of lotic systems is still in its infancy, and the "complex of factors which structure (stream communities) still needs to be elucidated" (Reice 1980).

## Methods

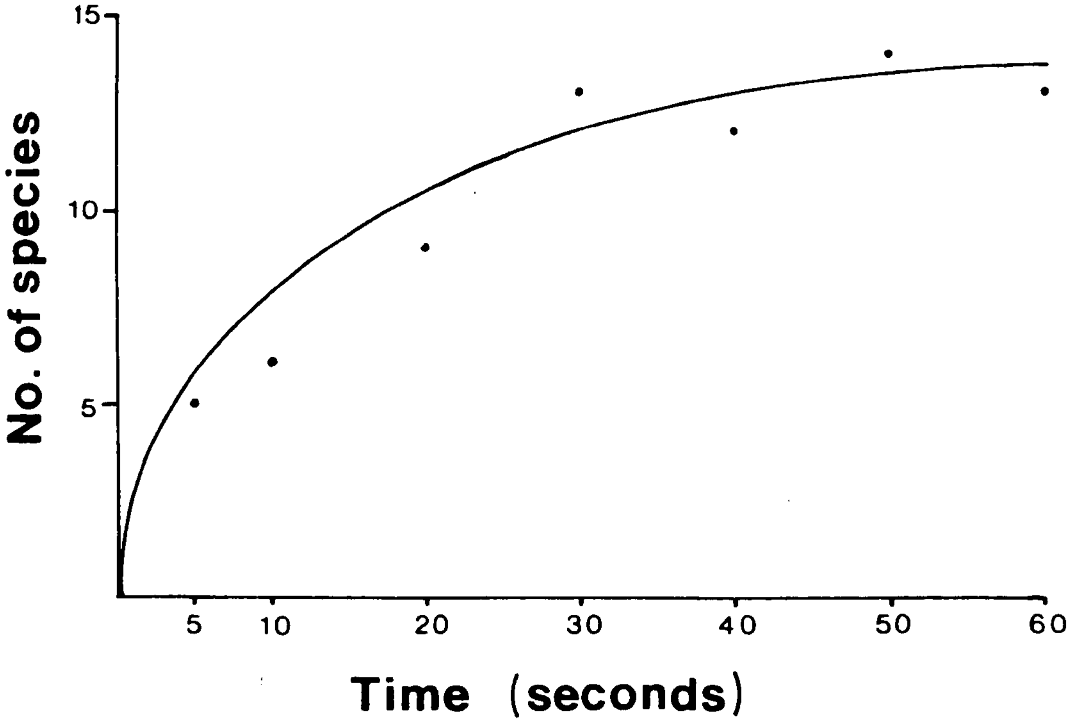
A wide variety of techniques and equipment is available for sampling lotic invertebrate communities. In choosing a suitable method, it is necessary to make a number of decisions concerning the nature of the sample to be obtained. Although qualitative samples were sufficient for the purposes of this study, the question of whether or not it is possible to obtain quantitative samples of the 'stream community' is debatable. Indeed Hynes (1970) implies that, of the techniques commonly employed, there is little to choose between them. The singular lack of a simple, statistically valid technique for estimating the

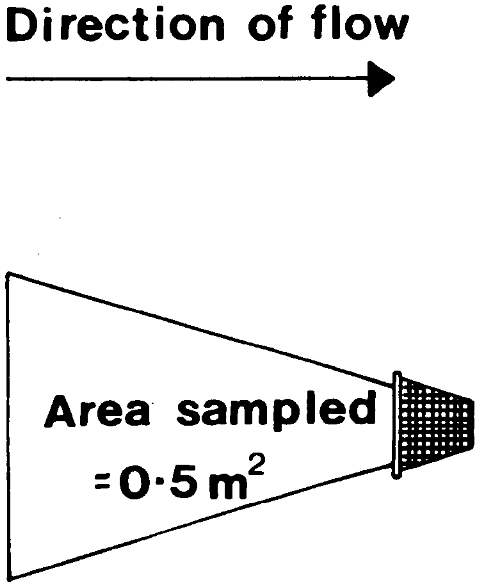
## FIGURE 8

Curve showing the relationship between duration of kick sample and number of species collected - optimal sampling time was estimated as 30 seconds.

## FIGURE 9

Diagram illustrating the area of the stream bed sampled in kick sampling, and the position of the net in relation to the direction of current flow.


15
10
5
No. of species
5
10
20
30
40
50
60
Time (seconds)


Direction of flow
Area sampled
=0·5 m²

abundance of benthic macroinvertebrates has proved to be a major obstacle in the advancement of this area of freshwater research. This matter receives further attention later in this section.

The technique uesd here is a slight modification of the kick sampling technique used by Morgan and Egglishaw (1965) in their study of Scottish upland stream faunas. This was chosen since it involved a minimum of time and effort to collect and analyse samples, it had proved successful in similar stream types, it sampled the community extensively, it was repeatable and it afforded a minimum of disturbance to the stations being sampled.

The execution of this sampling technique was similar to the description given in Morgan and Egglishaw (ibid.) with one major difference : The intensity of sampling was controlled by time rather than effort (i.e. number of 'kicks'). A sampling efficiency curve was constructed by assessing the number of species collected in similar samples of varying duration (Figure 8). The optimum sampling time was calculated as 30 seconds. The area of the substratum 'kicked' was a trapezoid of approximately 0.5m (Figure 9). The pore size of the net was approximately 1mm.

This technique proved unsuitable for station 5 (Fairy Loch), and in this case six 'standard sweeps' of the pond net were found to be an acceptable substitute for the normal procedure. The ephemeral nature of station 8 (the source) prevented kick sampling on a number of occasions, and no other method could be substituted in these circumstances. Net samples were transferred into 2l. polythene containers containing stream water, and were returned to the laboratory for immediate analysis. Here, samples were sieved in order to remove fine particulate material, and were decanted into a large tray pending sorting. Samples were sorted alive, under optimum illumination, into component species. The relative numbers of each species were recorded, with animals less than 2mm in length being discounted.

Animals were classified to species only when identification was absolutely certain. In identifying species, the following keys were used : General guides - Quigley (1977), Merritt and Cummins (1978); Oligochaeta - Brinkhurst (1971), Ladle (unpublished key to families); Nematomorpha - Ritchie (1915); Malacostraca - Gledhill et al. (1976); Odonata - Corbet et al. (1960 ); Megaloptera - Elliott (1977a);Plecoptera - Hynes (1977); Ephemeroptera - Macan (1979); Trichoptera (general) - Hickin (1967); Trichoptera (caseless) - Edington and Hildrew (1981); Trichoptera - Hiley (unpublished key to families); Hemiptera - Macan (1976); Coleoptera (Elminthidae) - Holland (1972); Tipulidae - Brindle (1960); Chironomidae - Pinder (unpublished key to larval subfamilies); Simuliidae - Davies (1968); other Diptera - Merritt and Cummins (1978); Gastropoda - Macan (1977); Bivalvia - Ellis (1978); Amphibia - Arnold et al. (1978). One vertebrate species was recorded (at station 5), and was included in the sample analysis.

| TAXA | 1980 | | | | | | | | | | 1981 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | M | A | M | J | J | A | S | O | N | D | J | F |
| PLATYHELMINTHES | | | | | | | | | | | | |
| Crenobia alpina | - | 003 | 011 | 002 | 001 | 003 | 002 | 003 | - | 001 | - | - |
| OLIGOCHAETA | | | | | | | | | | | | |
| Lumbricus terrestris | - | - | 004 | - | - | - | - | - | 001 | - | - | - |
| Lumbriculid sp. | - | 001 | 012 | - | - | - | - | 001 | 002 | 001 | - | - |
| NEMATOMORPHA | | | | | | | | | | | | |
| Gordius sp. | ABSENT | | | | | | | | | | | |
| AMPHIPODA | | | | | | | | | | | | |
| Gammarus pulex | 003 | 015 | 018 | 020 | 011 | 001 | 005 | 011 | 005 | 007 | 002 | 001 |
| ACARINA | | | | | | | | | | | | |
| Hydracarina | ABSENT | | | | | | | | | | | |
| ODONATA | | | | | | | | | | | | |
| Coenagrion puella | ABSENT | | | | | | | | | | | |
| PLECOPTERA | | | | | | | | | | | | |
| Brachyptera risi | - | - | - | - | - | - | - | 006 | - | 011 | 016 | 019 |
| Leuctra hippopus | ABSENT | | | | | | | | | | | |
| Amphinemura sulcicollis | ABSENT | | | | | | | | | | | |
| Nemurella picteti | ABSENT | | | | | | | | | | | |
| Isoperla grammatica | 015 | 004 | - | 008 | 007 | - | 001 | - | 038 | - | 004 | 001 |
| Dinocras cephalotes | - | 012 | 023 | 002 | - | - | 001 | 005 | 007 | 016 | 003 | - |
| Capnia atra | ABSENT | | | | | | | | | | | |
| EPHEMEROPTERA | | | | | | | | | | | | |
| Baetis rhodani/muticus | 005 | 005 | 008 | - | 010 | 002 | 002 | - | 002 | 002 | - | 001 |
| Rhithrogena semicolorata/germanica | - | - | 016 | 010 | 008 | - | 006 | 005 | 002 | 001 | 016 | 013 |
| DIPTERA | | | | | | | | | | | | |
| Chironomid spp. | ABSENT | | | | | | | | | | | |
| Ceratopogonid spp. | - | 002 | - | - | - | - | 004 | 002 | - | - | - | 002 |
| Simulium sp. | - | - | - | - | - | 001 | - | - | 002 | - | - | 006 |
| Dixa sp. | ABSENT | | | | | | | | | | | |
| Tipula/Dicranota spp. | 001 | 001 | 003 | - | - | - | - | 002 | 001 | 003 | 002 | 002 |
| TRICHOPTERA (caseless) | | | | | | | | | | | | |
| Diplectrona felix | 038 | 011 | 012 | 006 | 001 | 003 | 007 | 002 | 009 | 010 | 005 | 004 |
| Polycentropus flavomaculatus | 002 | - | - | - | - | - | - | - | 001 | - | - | - |
| Rhyacophila dorsalis | 002 | - | - | - | - | - | - | 001 | 002 | 001 | 002 | 004 |
| Philopotamus montanus | 007 | 004 | 004 | 001 | - | - | 002 | - | 010 | 001 | - | 001 |
| TRICHOPTERA (cased) | | | | | | | | | | | | |
| Potamophylax cingulatus | - | 001 | 004 | 004 | 003 | - | - | 001 | 002 | 006 | 002 | 006 |
| Limnephilid sp.2 | ABSENT | | | | | | | | | | | |
| Silo pallipes | ABSENT | | | | | | | | | | | |
| Goera pilosa | - | - | 001 | - | - | - | - | - | - | 007 | 001 | 002 |
| Arthripsodes sp. | - | - | - | - | 001 | - | - | 005 | 004 | - | 012 | - |
| HEMIPTERA | | | | | | | | | | | | |
| Cymatia bonsdorffi | ABSENT | | | | | | | | | | | |
| COLEOPTERA | | | | | | | | | | | | |
| Elmis aenea(ADULT) | - | - | 001 | - | - | - | - | - | - | - | - | - |
| Elmis aenea(LARVA) | 012 | 007 | - | - | - | - | - | 006 | 005 | 015 | - | - |
| Dytiscus marginalis(LARVA) | ABSENT | | | | | | | | | | | |
| Gyrinus sp.(ADULT) | ABSENT | | | | | | | | | | | |
| MEGALOPTERA | | | | | | | | | | | | |
| Sialis lutaria | ABSENT | | | | | | | | | | | |
| MOLLUSCA | | | | | | | | | | | | |
| Ancylus fluviatilis | - | - | 001 | - | - | - | 001 | - | - | - | - | - |
| Sphaeriid sp. | ABSENT | | | | | | | | | | | |
| AMPHIBIA | | | | | | | | | | | | |
| Salamandra atra | ABSENT | | | | | | | | | | | |
| TOTAL NOS. IN SAMPLE | 85 | 66 | 118 | 53 | 42 | 10 | 31 | 50 | 93 | 82 | 65 | 62 |
| TOTAL NO. OF TAXA ( = S ) | 9 | 12 | 14 | 8 | 6 | 5 | 10 | 13 | 16 | 14 | 11 | 13 |

TABLE 7 : NUMBERS OF ANIMALS IN MONTHLY KICK SAMPLES AT STATION 1 - SEE TEXT.

| TAXA | 1980 | | | | | | | | | | 1981 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | M | A | M | J | J | A | S | O | N | D | J | F |
| PLATYHELMINTHES | | | | | | | | | | | | |
| Crenobia alpina | - | - | - | - | - | - | 001 | - | - | - | 001 | - |
| OLIGOCHAETA | | | | | | | | | | | | |
| Lumbricus terrestris | ABSENT | | | | | | | | | | | |
| Lumbriculid sp. | - | - | - | - | - | 001 | 001 | 001 | 001 | - | 009 | - |
| NEMATOMORPHA | | | | | | | | | | | | |
| Gordius sp. | ABSENT | | | | | | | | | | | |
| AMPHIPODA | | | | | | | | | | | | |
| Gammarus pulex | 010 | 007 | 010 | 009 | - | - | 001 | 007 | 008 | 002 | 008 | 011 |
| ACARINA | | | | | | | | | | | | |
| Hydracarina | ABSENT | | | | | | | | | | | |
| ODONATA | | | | | | | | | | | | |
| Coenagrion puella | ABSENT | | | | | | | | | | | |
| PLECOPTERA | | | | | | | | | | | | |
| Brachyptera risi | - | - | - | - | - | - | 002 | 014 | - | 004 | 012 | 008 |
| Leuctra hippopus | - | - | - | - | - | - | - | 004 | 001 | - | - | 005 |
| Amphinemura sulcicollis | - | - | - | - | - | - | 001 | - | - | - | - | - |
| Nemurella picteti | ABSENT | | | | | | | | | | | |
| Isoperla grammatica | 009 | - | 004 | 002 | 004 | - | 002 | - | 011 | 009 | 011 | 006 |
| Dinocras cephalotes | - | 007 | 014 | 004 | - | 014 | - | 015 | 015 | 007 | 002 | 006 |
| Capnia atra | ABSENT | | | | | | | | | | | |
| EPHEMEROPTERA | | | | | | | | | | | | |
| Baetis rhodani/muticus | 011 | 001 | 004 | - | - | 003 | 010 | - | 002 | 003 | 001 | 002 |
| Rhithrogena semicolorata/germanica | - | - | 013 | 006 | 006 | 002 | - | - | - | 001 | 007 | 002 |
| DIPTERA | | | | | | | | | | | | |
| Chironomid spp. | ABSENT | | | | | | | | | | | |
| Ceratopogonid spp. | - | 002 | - | - | - | 003 | 003 | - | - | 001 | 002 | - |
| Simulium sp. | - | - | - | - | 004 | - | 007 | - | - | 001 | 003 | - |
| Dixa sp. | ABSENT | | | | | | | | | | | |
| Tipula/Dicranota spp. | - | 001 | 003 | 005 | 002 | - | - | - | 003 | 002 | 004 | 002 |
| TRICHOPTERA (caseless) | | | | | | | | | | | | |
| Diplectrona felix | 011 | 007 | 001 | 003 | - | 008 | 001 | 005 | 001 | 002 | 004 | 002 |
| Polycentropus flavomaculatus | 002 | - | 001 | 004 | 011 | - | - | - | 001 | - | 005 | 002 |
| Rhyacophila dorsalis | - | - | - | - | - | 001 | - | - | 002 | - | - | - |
| Philopotamus montanus | 018 | 002 | 001 | 002 | - | 023 | - | 010 | 013 | 001 | 002 | 001 |
| TRICHOPTERA (cased) | | | | | | | | | | | | |
| Potamophylax cingulatus | - | - | - | 004 | 003 | - | - | - | - | - | - | - |
| Limnephilid sp.2 | ABSENT | | | | | | | | | | | |
| Silo pallipes | - | - | 001 | - | - | 002 | - | - | - | - | - | - |
| Goera pilosa | ABSENT | | | | | | | | | | | |
| Arthripsodes sp. | ABSENT | | | | | | | | | | | |
| HEMIPTERA | | | | | | | | | | | | |
| Cymatia bonsdorffi | ABSENT | | | | | | | | | | | |
| COLEOPTERA | | | | | | | | | | | | |
| Elmis aenea (ADULT) | - | - | 002 | - | - | 001 | - | - | 001 | - | 001 | - |
| Elmis aenea (LARVA) | - | 006 | - | - | 006 | 001 | - | 008 | 006 | 001 | 002 | - |
| Dytiscus marginalis (LARVA) | ABSENT | | | | | | | | | | | |
| Gyrinus sp. (ADULT) | ABSENT | | | | | | | | | | | |
| MEGALOPTERA | | | | | | | | | | | | |
| Sialis lutaria | ABSENT | | | | | | | | | | | |
| MOLLUSCA | | | | | | | | | | | | |
| Ancylus fluviatilis | - | - | - | - | - | 001 | - | - | - | - | - | - |
| Sphaeriid sp. | ABSENT | | | | | | | | | | | |
| AMPHIBIA | | | | | | | | | | | | |
| Salamandra atra | ABSENT | | | | | | | | | | | |
| TOTAL NOS. IN SAMPLE | 61 | 33 | 54 | 39 | 36 | 60 | 29 | 64 | 65 | 34 | 74 | 47 |
| TOTAL NO. OF TAXA ( = S ) | 6 | 8 | 11 | 9 | 7 | 12 | 10 | 8 | 13 | 12 | 16 | 11 |

TABLE 8 : NUMBERS OF ANIMALS IN MONTHLY KICK SAMPLES AT STATION 2 - SEE TEXT.

| TAXA | 1980 | | | | | | | | | | 1981 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | M | A | M | J | J | A | S | O | N | D | J | F |
| PLATYHELMINTHES | | | | | | | | | | | | |
| *Crenobia alpina* | - | - | - | 002 | - | 001 | 002 | 002 | - | 001 | 002 | 006 |
| OLIGOCHAETA | | | | | | | | | | | | |
| *Lumbricus terrestris* | - | - | - | - | - | - | - | - | - | - | - | 001 |
| *Lumbriculid sp.* | - | - | - | - | - | - | 001 | 001 | - | - | - | - |
| NEMATOMORPHA | | | | | | | | | | | | |
| *Gordius sp.* | ABSENT | | | | | | | | | | | |
| AMPHIPODA | | | | | | | | | | | | |
| *Gammarus pulex* | 024 | 051 | 038 | 021 | 004 | 015 | 014 | 036 | 008 | 028 | 011 | 012 |
| ACARINA | | | | | | | | | | | | |
| Hydracarina | ABSENT | | | | | | | | | | | |
| ODONATA | | | | | | | | | | | | |
| *Coenagrion puella* | ABSENT | | | | | | | | | | | |
| PLECOPTERA | | | | | | | | | | | | |
| *Brachyptera risi* | - | - | - | - | 006 | - | - | 012 | - | 013 | 002 | 001 |
| *Leuctra hippopus* | - | - | - | - | - | 001 | - | - | - | - | - | - |
| *Amphinemura sulcicollis* | - | - | - | - | - | 005 | - | - | - | - | - | - |
| *Nemurella picteti* | ABSENT | | | | | | | | | | | |
| *Isoperla grammatica* | 005 | 002 | - | 002 | 006 | 005 | 002 | - | 040 | - | 003 | 005 |
| *Dinocras cephalotes* | - | 004 | 013 | 001 | - | - | - | - | 007 | 004 | - | - |
| *Capnia atra* | ABSENT | | | | | | | | | | | |
| EPHEMEROPTERA | | | | | | | | | | | | |
| *Baetis rhodani/muticus* | - | - | 001 | 003 | - | 002 | 001 | - | 002 | - | - | - |
| *Rhithrogena semicolorata/germanica* | - | - | 002 | - | - | - | 001 | - | 006 | - | 002 | - |
| DIPTERA | | | | | | | | | | | | |
| *Chironomid spp.* | ABSENT | | | | | | | | | | | |
| *Ceratopogonid spp.* | ABSENT | | | | | | | | | | | |
| *Simulium sp.* | - | - | 001 | - | - | - | - | - | - | - | 001 | - |
| *Dixa sp.* | ABSENT | | | | | | | | | | | |
| *Tipula/Dicranota spp.* | 007 | - | 002 | 002 | - | 001 | 001 | 006 | 001 | 002 | 003 | 002 |
| TRICHOPTERA (caseless) | | | | | | | | | | | | |
| *Diplectrona felix* | 003 | - | - | - | 001 | 002 | - | 005 | 001 | 003 | 001 | 001 |
| *Polycentropus flavomaculatus* | 014 | 024 | 003 | 007 | 007 | 002 | - | 001 | - | 003 | - | 001 |
| *Rhyacophila dorsalis* | - | 001 | 001 | - | - | - | 003 | - | - | 003 | - | - |
| *Philopotamus montanus* | 086 | 012 | - | - | - | - | 002 | 003 | - | - | - | - |
| TRICHOPTERA (cased) | | | | | | | | | | | | |
| *Potamophylax cingulatus* | - | - | 001 | 001 | 003 | - | 007 | 002 | 001 | 002 | - | - |
| *Limnephilid sp.2* | ABSENT | | | | | | | | | | | |
| *Silo pallipes* | - | - | 006 | - | - | - | - | - | - | 005 | - | - |
| *Goera pilosa* | - | - | - | 001 | 004 | - | - | 002 | - | 004 | 001 | - |
| *Arthripsodes sp.* | ABSENT | | | | | | | | | | | |
| HEMIPTERA | | | | | | | | | | | | |
| *Cymatia bonsdorffi* | ABSENT | | | | | | | | | | | |
| COLEOPTERA | | | | | | | | | | | | |
| *Elmis aenea*(ADULT) | - | - | - | 002 | 001 | 001 | - | - | - | - | - | - |
| *Elmis aenea*(LARVA) | - | - | - | - | 001 | - | - | 002 | 001 | - | - | - |
| *Dytiscus marginalis*(LARVA) | ABSENT | | | | | | | | | | | |
| *Gyrinus sp.*(ADULT) | ABSENT | | | | | | | | | | | |
| MEGALOPTERA | | | | | | | | | | | | |
| *Sialis lutaria* | ABSENT | | | | | | | | | | | |
| MOLLUSCA | | | | | | | | | | | | |
| *Ancylus fluviatilis* | - | - | - | - | - | 002 | - | - | - | - | - | - |
| *Sphaeriid sp.* | ABSENT | | | | | | | | | | | |
| AMPHIBIA | | | | | | | | | | | | |
| *Salamandra atra* | ABSENT | | | | | | | | | | | |
| TOTAL NOS. IN SAMPLE | 139 | 94 | 68 | 42 | 33 | 37 | 34 | 72 | 67 | 69 | 26 | 29 |
| TOTAL NO. OF TAXA ( = S ) | 6 | 6 | 10 | 10 | 9 | 11 | 10 | 11 | 9 | 11 | 9 | 8 |

TABLE 9 : NUMBERS OF ANIMALS IN MONTHLY KICK SAMPLES AT STATION 3 - SEE TEXT.

| TAXA | 1980 | | | | | | | | | | 1981 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | M | A | M | J | J | A | S | O | N | D | J | F |
| PLATYHELMINTHES | | | | | | | | | | | | |
| *Crenobia alpina* | 003 | - | 002 | - | - | - | - | 001 | - | 004 | 004 | 001 |
| OLIGOCHAETA | | | | | | | | | | | | |
| *Lumbricus terrestris* | ABSENT | | | | | | | | | | | |
| *Lumbriculid sp.* | ABSENT | | | | | | | | | | | |
| NEMATOMORPHA | | | | | | | | | | | | |
| *Gordius sp.* | ABSENT | | | | | | | | | | | |
| AMPHIPODA | | | | | | | | | | | | |
| *Gammarus pulex* | 017 | 013 | 023 | 008 | 014 | 010 | 013 | 005 | 003 | 016 | 020 | 007 |
| ACARINA | | | | | | | | | | | | |
| Hydracarina | ABSENT | | | | | | | | | | | |
| ODONATA | | | | | | | | | | | | |
| *Coenagrion puella* | ABSENT | | | | | | | | | | | |
| PLECOPTERA | | | | | | | | | | | | |
| *Brachyptera risi* | 001 | - | 003 | 007 | 003 | - | - | 009 | - | 002 | 005 | 004 |
| *Leuctra hippopus* | - | - | - | - | 001 | - | - | 001 | - | - | - | 003 |
| *Amphinemura sulcicollis* | - | - | - | - | - | - | 002 | - | - | - | - | 001 |
| *Nemurella picteti* | ABSENT | | | | | | | | | | | |
| *Isoperla grammatica* | - | - | - | - | 004 | 003 | - | - | 003 | 001 | 004 | 002 |
| *Dinocras cephalotes* | - | 004 | 008 | - | - | - | - | 001 | 001 | 002 | - | - |
| *Capnia atra* | ABSENT | | | | | | | | | | | |
| EPHEMEROPTERA | | | | | | | | | | | | |
| *Baetis rhodani/muticus* | 001 | 001 | 009 | - | 017 | 002 | 017 | 002 | - | - | 004 | - |
| *Rhithrogena semicolorata/germanica* | - | - | 013 | 014 | 008 | 002 | 001 | - | 004 | 001 | 009 | 003 |
| DIPTERA | | | | | | | | | | | | |
| *Chironomid spp.* | ABSENT | | | | | | | | | | | |
| *Ceratopogonid spp.* | ABSENT | | | | | | | | | | | |
| *Simulium sp.* | ABSENT | | | | | | | | | | | |
| *Dixa sp.* | - | - | 001 | - | - | - | - | - | - | 001 | - | - |
| *Tipula/Dicranota spp.* | 001 | 002 | 001 | 002 | - | - | - | 002 | - | 001 | 001 | - |
| TRICHOPTERA (caseless) | | | | | | | | | | | | |
| *Diplectrona felix* | - | - | - | 002 | - | - | - | - | - | - | - | - |
| *Polycentropus flavomaculatus* | 001 | 001 | - | - | - | - | 001 | 001 | - | - | - | 001 |
| *Rhyacophila dorsalis* | - | - | 004 | 001 | - | - | 001 | - | - | 001 | 003 | 007 |
| *Philopotamus montanus* | - | 013 | 001 | - | - | - | 003 | - | - | 001 | 001 | - |
| TRICHOPTERA (cased) | | | | | | | | | | | | |
| *Potamophylax cingulatus* | 002 | - | 001 | - | - | - | - | - | 001 | - | 001 | 005 |
| *Limnephilid sp.2* | ABSENT | | | | | | | | | | | |
| *Silo pallipes* | - | - | - | 008 | - | - | - | - | - | - | - | - |
| *Goera pilosa* | 003 | - | - | - | - | - | - | - | - | - | - | - |
| *Arthripsodes sp.* | - | - | 001 | - | 001 | - | 001 | 003 | 001 | 004 | - | 004 |
| HEMIPTERA | | | | | | | | | | | | |
| *Cymatia bonsdorffi* | ABSENT | | | | | | | | | | | |
| COLEOPTERA | | | | | | | | | | | | |
| *Elmis aenea*(ADULT) | ABSENT | | | | | | | | | | | |
| *Elmis aenea*(LARVA) | 001 | 004 | - | 001 | - | - | - | - | - | 001 | 001 | - |
| *Dytiscus marginalis*(LARVA) | ABSENT | | | | | | | | | | | |
| *Gyrinus sp.*(ADULT) | ABSENT | | | | | | | | | | | |
| MEGALOPTERA | | | | | | | | | | | | |
| *Sialis lutaria* | ABSENT | | | | | | | | | | | |
| MOLLUSCA | | | | | | | | | | | | |
| *Ancylus fluviatilis* | 003 | 007 | - | - | - | - | - | - | - | - | - | - |
| *Sphaeriid sp.* | ABSENT | | | | | | | | | | | |
| AMPHIBIA | | | | | | | | | | | | |
| *Salamandra atra* | ABSENT | | | | | | | | | | | |
| TOTAL NOS. IN SAMPLE | 33 | 45 | 67 | 43 | 48 | 17 | 39 | 25 | 13 | 35 | 53 | 38 |
| TOTAL NO. OF TAXA ( = S ) | 10 | 8 | 12 | 8 | 7 | 4 | 8 | 9 | 6 | 12 | 11 | 11 |

TABLE 10 : NUMBERS OF ANIMALS IN MONTHLY KICK SAMPLES AT STATION 4 - SEE TEXT.

| TAXA | 1980 | | | | | | | | | | 1981 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | M | A | M | J | J | A | S | O | N | D | J | F |
| PLATYHELMINTHES | | | | | | | | | | | | |
| Crenobia alpina | ABSENT | | | | | | | | | | | |
| OLIGOCHAETA | | | | | | | | | | | | |
| Lumbricus terrestris | ABSENT | | | | | | | | | | | |
| Lumbriculid sp. | - | - | - | 002 | 003 | 004 | - | - | 001 | 002 | * | * |
| NEMATOMORPHA | | | | | | | | | | | | |
| Gordius sp. | ABSENT | | | | | | | | | | | |
| AMPHIPODA | | | | | | | | | | | | |
| Gammarus pulex | 069 | 187 | 187 | 111 | 028 | 016 | 008 | 016 | 013 | 008 | * | * |
| ACARINA | | | | | | | | | | | | |
| Hydracarina | - | - | 014 | - | - | - | - | - | - | - | * | * |
| ODONATA | | | | | | | | | | | | |
| Coenagrion puella | - | - | - | 001 | - | - | - | - | 002 | - | * | * |
| PLECOPTERA | | | | | | | | | | | | |
| Brachyptera risi | ABSENT | | | | | | | | | | | |
| Leuctra hippopus | ABSENT | | | | | | | | | | | |
| Amphinemura sulcicollis | ABSENT | | | | | | | | | | | |
| Nemurella picteti | 503 | 632 | 1026 | 1532 | 128 | 645 | 574 | 165 | 173 | 523 | * | * |
| Isoperla grammatica | ABSENT | | | | | | | | | | | |
| Dinocras cephalotes | ABSENT | | | | | | | | | | | |
| Capnia atra | ABSENT | | | | | | | | | | | |
| EPHEMEROPTERA | | | | | | | | | | | | |
| Baetis rhodani/muticus | ABSENT | | | | | | | | | | | |
| Rhithrogena semicolorata/germanica | ABSENT | | | | | | | | | | | |
| DIPTERA | | | | | | | | | | | | |
| Chironomid spp. | 187 | 310 | 567 | 062 | 090 | 008 | 006 | 036 | 076 | 010 | * | * |
| Ceratopogonid spp. | ABSENT | | | | | | | | | | | |
| Simulium sp. | ABSENT | | | | | | | | | | | |
| Dixa sp. | ABSENT | | | | | | | | | | | |
| Tipula/Dicranota spp. | ABSENT | | | | | | | | | | | |
| TRICHOPTERA (caseless) | | | | | | | | | | | | |
| Diplectrona felix | ABSENT | | | | | | | | | | | |
| Polycentropus flavomaculatus | 002 | - | 001 | - | - | 004 | - | - | 004 | 002 | * | * |
| Rhyacophila dorsalis | ABSENT | | | | | | | | | | | |
| Philopotamus montanus | ABSENT | | | | | | | | | | | |
| TRICHOPTERA (cased) | | | | | | | | | | | | |
| Potamophylax cingulatus | ABSENT | | | | | | | | | | | |
| Limnephilid sp.2 | - | - | - | - | - | - | - | - | 001 | - | * | * |
| Silo pallipes | ABSENT | | | | | | | | | | | |
| Goera pilosa | ABSENT | | | | | | | | | | | |
| Arthripsodes sp. | - | - | - | - | - | 001 | 002 | - | - | - | * | * |
| HEMIPTERA | | | | | | | | | | | | |
| Cymatia bonsdorffi | 001 | - | - | - | - | - | 001 | - | - | - | * | * |
| COLEOPTERA | | | | | | | | | | | | |
| Elmis aenea(ADULT) | ABSENT | | | | | | | | | | | |
| Elmis aenea(LARVA) | - | 009 | - | 002 | 007 | - | - | - | - | - | * | * |
| Dytiscus marginalis(LARVA) | 003 | 007 | - | - | - | 001 | - | - | - | - | * | * |
| Gyrinus sp.(ADULT) | - | - | - | 001 | - | - | - | 001 | - | - | * | * |
| MEGALOPTERA | | | | | | | | | | | | |
| Sialis lutaria | - | - | - | 001 | - | - | - | - | 001 | - | * | * |
| MOLLUSCA | | | | | | | | | | | | |
| Ancylus fluviatilis | 027 | 001 | 001 | - | 003 | - | 001 | - | - | - | * | * |
| Sphaeriid sp. | - | - | 006 | - | 047 | 004 | - | 010 | 014 | 020 | * | * |
| AMPHIBIA | | | | | | | | | | | | |
| Salamandra atra | 004 | - | - | 004 | - | - | - | 001 | - | - | * | * |
| TOTAL NOS. IN SAMPLE | 796 | 1146 | 1802 | 1716 | 306 | 683 | 592 | 229 | 285 | 565 | * | * |
| TOTAL NO. OF TAXA ( = S ) | 8 | 6 | 7 | 9 | 7 | 8 | 6 | 6 | 9 | 6 | * | * |

**TABLE 11 : NUMBERS OF ANIMALS IN MONTHLY KICK SAMPLES AT STATION 5 - SEE TEXT. (*=missing data)**

| TAXA | 1980 | | | | | | | | | | 1981 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | M | A | M | J | J | A | S | O | N | D | J | F |
| PLATYHELMINTHES | | | | | | | | | | | | |
| Crenobia alpina | - | 006 | 009 | 019 | 009 | 009 | 007 | 014 | - | 002 | 007 | 006 |
| OLIGOCHAETA | | | | | | | | | | | | |
| Lumbricus terrestris | ABSENT | | | | | | | | | | | |
| Lumbriculid sp. | ABSENT | | | | | | | | | | | |
| NEMATOMORPHA | | | | | | | | | | | | |
| Gordius sp. | ABSENT | | | | | | | | | | | |
| AMPHIPODA | | | | | | | | | | | | |
| Gammarus pulex | 064 | 042 | 067 | 018 | 036 | 009 | 036 | 031 | 006 | 013 | 028 | 052 |
| ACARINA | | | | | | | | | | | | |
| Hydracarina | ABSENT | | | | | | | | | | | |
| ODONATA | | | | | | | | | | | | |
| Coenagrion puella | ABSENT | | | | | | | | | | | |
| PLECOPTERA | | | | | | | | | | | | |
| Brachyptera risi | - | - | 001 | - | - | - | - | 001 | - | - | - | - |
| Leuctra hippopus | ABSENT | | | | | | | | | | | |
| Amphinemura sulcicollis | ABSENT | | | | | | | | | | | |
| Nemurella picteti | 002 | 028 | 002 | - | 007 | 004 | - | - | - | - | - | - |
| Isoperla grammatica | ABSENT | | | | | | | | | | | |
| Dinocras cephalotes | - | - | - | - | - | 003 | - | 001 | - | - | - | - |
| Capnia atra | - | - | - | 014 | 007 | 004 | - | 002 | - | - | 003 | - |
| EPHEMEROPTERA | | | | | | | | | | | | |
| Baetis rhodani/muticus | - | - | - | - | - | - | - | - | 001 | - | - | - |
| Rhithrogena semicolorata/germanica | ABSENT | | | | | | | | | | | |
| DIPTERA | | | | | | | | | | | | |
| Chironomid spp. | - | - | - | - | 004 | 006 | - | - | - | - | - | - |
| Ceratopogonid spp. | - | - | - | - | - | - | 001 | - | 002 | - | - | - |
| Simulium sp. | - | 001 | - | - | - | - | - | - | - | - | - | - |
| Dixa sp. | - | - | 001 | - | 001 | - | 002 | 001 | - | - | 002 | 001 |
| Tipula/Dicranota spp. | - | 002 | 001 | - | - | - | - | - | - | - | - | - |
| TRICHOPTERA (caseless) | | | | | | | | | | | | |
| Diplectrona felix | - | - | - | - | - | 004 | - | - | - | - | - | - |
| Polycentropus flavomaculatus | ABSENT | | | | | | | | | | | |
| Rhyacophila dorsalis | ABSENT | | | | | | | | | | | |
| Philopotamus montanus | - | - | 008 | 007 | 002 | 001 | 001 | - | 001 | - | 004 | 005 |
| TRICHOPTERA (cased) | | | | | | | | | | | | |
| Potamophylax cingulatus | ABSENT | | | | | | | | | | | |
| Limnephilid sp.2 | - | 006 | 004 | 005 | 014 | 008 | 001 | 001 | - | 007 | 002 | - |
| Silo pallipes | - | - | - | - | - | - | - | - | - | - | 001 | 005 |
| Goera pilosa | - | - | - | - | - | 002 | 001 | - | 006 | 004 | 001 | - |
| Arthripsodes sp. | ABSENT | | | | | | | | | | | |
| HEMIPTERA | | | | | | | | | | | | |
| Cymatia bonsdorffi | ABSENT | | | | | | | | | | | |
| COLEOPTERA | | | | | | | | | | | | |
| Elmis aenea (ADULT) | ABSENT | | | | | | | | | | | |
| Elmis aenea (LARVA) | 011 | 002 | 002 | - | 001 | 003 | 003 | 001 | - | 001 | - | - |
| Dytiscus marginalis (LARVA) | ABSENT | | | | | | | | | | | |
| Gyrinus sp. (ADULT) | ABSENT | | | | | | | | | | | |
| MEGALOPTERA | | | | | | | | | | | | |
| Sialis lutaria | ABSENT | | | | | | | | | | | |
| MOLLUSCA | | | | | | | | | | | | |
| Ancylus fluviatilis | ABSENT | | | | | | | | | | | |
| Sphaeriid sp. | ABSENT | | | | | | | | | | | |
| AMPHIBIA | | | | | | | | | | | | |
| Salamandra atra | ABSENT | | | | | | | | | | | |
| TOTAL NOS. IN SAMPLE | 77 | 85 | 95 | 63 | 81 | 53 | 52 | 52 | 16 | 27 | 49 | 69 |
| TOTAL NO. OF TAXA ( = S ) | 3 | 7 | 9 | 5 | 9 | 11 | 8 | 8 | 5 | 5 | 9 | 5 |

TABLE 12 : NUMBERS OF ANIMALS IN MONTHLY KICK SAMPLES AT STATION 6 - SEE TEXT.

| TAXA | 1980 | | | | | | | | | | 1981 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | M | A | M | J | J | A | S | O | N | D | J | F |
| PLATYHELMINTHES | | | | | | | | | | | | |
| Crenobia alpina | ABSENT | | | | | | | | | | | |
| OLIGOCHAETA | | | | | | | | | | | | |
| Lumbricus terrestris | ABSENT | | | | | | | | | | | |
| Lumbriculid sp. | ABSENT | | | | | | | | | | | |
| NEMATOMORPHA | | | | | | | | | | | | |
| Gordius sp. | ABSENT | | | | | | | | | | | |
| AMPHIPODA | | | | | | | | | | | | |
| Gammarus pulex | * | * | 047 | 035 | 004 | 009 | 104 | 042 | 022 | * | 031 | 014 |
| ACARINA | | | | | | | | | | | | |
| Hydracarina | ABSENT | | | | | | | | | | | |
| ODONATA | | | | | | | | | | | | |
| Coenagrion puella | ABSENT | | | | | | | | | | | |
| PLECOPTERA | | | | | | | | | | | | |
| Brachyptera risi | ABSENT | | | | | | | | | | | |
| Leuctra hippopus | ABSENT | | | | | | | | | | | |
| Amphinemura sulcicollis | ABSENT | | | | | | | | | | | |
| Nemurella picteti | * | * | 003 | 001 | - | - | - | 014 | - | * | - | 002 |
| Isoperla grammatica | * | * | - | - | 002 | 001 | - | - | 004 | * | 002 | 002 |
| Dinocras cephalotes | * | * | - | - | - | - | - | - | 005 | * | - | - |
| Capnia atra | * | * | 008 | 001 | - | - | - | - | 007 | * | - | - |
| EPHEMEROPTERA | | | | | | | | | | | | |
| Baetis rhodani/muticus | * | * | 001 | - | 001 | 004 | - | - | - | * | - | - |
| Rhithrogena semicolorata/germanica | ABSENT | | | | | | | | | | | |
| DIPTERA | | | | | | | | | | | | |
| Chironomid spp. | ABSENT | | | | | | | | | | | |
| Ceratopogonid spp. | * | * | - | - | 006 | - | - | - | - | * | 001 | - |
| Simulium sp. | ABSENT | | | | | | | | | | | |
| Dixa sp. | ABSENT | | | | | | | | | | | |
| Tipula/Dicranota spp. | * | * | 002 | - | - | 006 | - | - | 003 | * | 003 | 002 |
| TRICHOPTERA (caseless) | | | | | | | | | | | | |
| Diplectrona felix | * | * | - | - | - | 003 | 005 | 009 | 003 | * | 017 | 001 |
| Polycentropus flavomaculatus | ABSENT | | | | | | | | | | | |
| Rhyacophila dorsalis | * | * | - | - | - | - | - | 001 | - | * | - | 001 |
| Philopotamus montanus | * | * | - | - | - | 001 | - | - | - | * | 005 | - |
| TRICHOPTERA (cased) | | | | | | | | | | | | |
| Potamophylax cingulatus | ABSENT | | | | | | | | | | | |
| Limnephilid sp.2 | * | * | 005 | 002 | - | - | 007 | - | 008 | * | 012 | 001 |
| Silo pallipes | * | * | - | - | 002 | 012 | - | 001 | - | * | - | 003 |
| Goera pilosa | * | * | - | - | - | - | - | - | - | * | 001 | 002 |
| Arthripsodes sp. | * | * | - | - | - | 005 | - | - | 002 | * | 005 | 001 |
| HEMIPTERA | | | | | | | | | | | | |
| Cymatia bonsdorffi | ABSENT | | | | | | | | | | | |
| COLEOPTERA | | | | | | | | | | | | |
| Elmis aenea(ADULT) | ABSENT | | | | | | | | | | | |
| Elmis aenea(LARVA) | * | * | 001 | - | - | - | 003 | 002 | - | * | 005 | - |
| Dytiscus marginalis(LARVA) | ABSENT | | | | | | | | | | | |
| Gyrinus sp.(ADULT) | ABSENT | | | | | | | | | | | |
| MEGALOPTERA | | | | | | | | | | | | |
| Sialis lutaria | ABSENT | | | | | | | | | | | |
| MOLLUSCA | | | | | | | | | | | | |
| Ancylus fluviatilis | ABSENT | | | | | | | | | | | |
| Sphaeriid sp. | ABSENT | | | | | | | | | | | |
| AMPHIBIA | | | | | | | | | | | | |
| Salamandra atra | ABSENT | | | | | | | | | | | |
| TOTAL NOS. IN SAMPLE | * | * | 67 | 39 | 15 | 41 | 119 | 69 | 54 | * | 82 | 29 |
| TOTAL NO. OF TAXA ( = S ) | * | * | 7 | 4 | 5 | 8 | 4 | 6 | 8 | * | 10 | 10 |

TABLE 13 : NUMBERS OF ANIMALS IN MONTHLY KICK SAMPLES AT STATION 7 - SEE TEXT. (*=missing data) %

| TAXA | | | | | 1980 | | | | | | 1981 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | M | A | M | J | J | A | S | O | N | D | J | F |
| PLATYHELMINTHES | | | | | | | | | | | | |
| *Crenobia alpina* | ABSENT | | | | | | | | | | | |
| OLIGOCHAETA | | | | | | | | | | | | |
| *Lumbricus terrestris* | ABSENT | | | | | | | | | | | |
| *Lumbriculid sp.* | - | * | - | - | * | * | * | - | 001 | * | * | * |
| NEMATOMORPHA | | | | | | | | | | | | |
| *Gordius sp.* | ABSENT | | | | | | | | | | | |
| AMPHIPODA | | | | | | | | | | | | |
| *Gammarus pulex* | 056 | * | 123 | 036 | * | * | * | 022 | 006 | * | * | * |
| ACARINA | | | | | | | | | | | | |
| Hydracarina | - | * | 001 | - | * | * | * | - | - | * | * | * |
| ODONATA | | | | | | | | | | | | |
| *Coenagrion puella* | ABSENT | | | | | | | | | | | |
| PLECOPTERA | | | | | | | | | | | | |
| *Brachyptera risi* | ABSENT | | | | | | | | | | | |
| *Leuctra hippopus* | ABSENT | | | | | | | | | | | |
| *Amphinemura sulcicollis* | ABSENT | | | | | | | | | | | |
| *Nemurella picteti* | 037 | * | 046 | 020 | * | * | * | - | 003 | * | * | * |
| *Isoperla grammatica* | ABSENT | | | | | | | | | | | |
| *Dinocras cephalotes* | ABSENT | | | | | | | | | | | |
| *Capnia atra* | ABSENT | | | | | | | | | | | |
| EPHEMEROPTERA | | | | | | | | | | | | |
| *Baetis rhodani/muticus* | ABSENT | | | | | | | | | | | |
| *Rhithrogena semicolorata/germanica* | ABSENT | | | | | | | | | | | |
| DIPTERA | | | | | | | | | | | | |
| *Chironomid spp.* | ABSENT | | | | | | | | | | | |
| *Ceratopogonid spp.* | ABSENT | | | | | | | | | | | |
| *Simulium sp.* | ABSENT | | | | | | | | | | | |
| *Dixa sp.* | ABSENT | | | | | | | | | | | |
| *Tipula/Dicranota spp.* | - | * | - | - | * | * | * | - | 003 | * | * | * |
| TRICHOPTERA (caseless) | | | | | | | | | | | | |
| *Diplectrona felix* | ABSENT | | | | | | | | | | | |
| *Polycentropus flavomaculatus* | - | * | 001 | - | * | * | * | - | - | * | * | * |
| *Rhyacophila dorsalis* | ABSENT | | | | | | | | | | | |
| *Philopotamus montanus* | ABSENT | | | | | | | | | | | |
| TRICHOPTERA (cased) | | | | | | | | | | | | |
| *Potamophylax cingulatus* | - | * | 006 | - | * | * | * | - | - | * | * | * |
| *Limnephilid sp.2* | - | * | - | - | * | * | * | 002 | - | * | * | * |
| *Silo pallipes* | ABSENT | | | | | | | | | | | |
| *Goera pilosa* | 016 | * | - | - | * | * | * | - | 002 | * | * | * |
| *Arthripsodes sp.* | ABSENT | | | | | | | | | | | |
| HEMIPTERA | | | | | | | | | | | | |
| *Cymatia bonsdorffi* | ABSENT | | | | | | | | | | | |
| COLEOPTERA | | | | | | | | | | | | |
| *Elmis aenea*(ADULT) | - | * | - | - | * | * | * | 009 | 002 | * | * | * |
| *Elmis aenea*(LARVA) | 005 | * | - | - | * | * | * | - | - | * | * | * |
| *Dytiscus marginalis*(LARVA) | ABSENT | | | | | | | | | | | |
| *Gyrinus sp.*(ADULT) | ABSENT | | | | | | | | | | | |
| MEGALOPTERA | | | | | | | | | | | | |
| *Sialis lutaria* | ABSENT | | | | | | | | | | | |
| MOLLUSCA | | | | | | | | | | | | |
| *Ancylus fluviatilis* | ABSENT | | | | | | | | | | | |
| *Sphaeriid sp.* | - | * | 024 | - | * | * | * | - | - | * | * | * |
| AMPHIBIA | | | | | | | | | | | | |
| *Salamandra atra* | ABSENT | | | | | | | | | | | |
| TOTAL NOS. IN SAMPLE | 114 | * | 201 | 56 | * | * | * | 33 | 17 | * | * | * |
| TOTAL NO. OF TAXA ( = S ) | 4 | * | 6 | 2 | * | * | * | 3 | 6 | * | * | * |

**TABLE 14 : NUMBERS OF ANIMALS IN MONTHLY KICK SAMPLES AT STATION 8 - SEE TEXT. (*=missing data)**

Samples were collected on a monthly basis at each station, when possible, over the period March 1980 to February 1981.

## Results

### (a)species composition and abundance

Data obtained from monthly samples are presented for stations 1-8 in Tables 7-14 respectively. Forty taxa were identified, three of which were not stream-dwellers (i.e. found only at station 5). The general composition of the fauna compared well with the faunal lists obtained by Morgan and Egglishaw (1965) for similar stream types. For all monthly samples, the total number of taxa recorded was greater in the downstream stations (1-4) than in the upstream stations (6-8) throughout the sampling period. This was typified by the Trichoptera. In the downstream area, caseless caddis were more abundant than in the upstream area. Polycentropus flavomaculatus was present at all the downstream stations, but was absent in upstream stations 6 and 7, and was only present in small numbers at station 8. Similar species present downstream and absent upstream included the cased caddis species Potamophylax cingulatus, which was 'replaced' upstream by the confamilial species 'limnephilid species 2' (unidentified to species), and the stonefly Amphinemura sulcicollis, which was similarly 'replaced' by the confamilial species Nemurella picteti. Obvious faunal differences existed between the two areas, therefore, and in order to gain insight into the potential causal reasons for these differences (such as the relationship between trichopteran species and flow rate mentioned earlier) further analyses were required.

### (b)site similarity

A comparison of the faunal similarity / difference involved the conversion of the data presented in Tables 7-14 into binary form (i.e. presence / absence data). It has often been argued that the use of binary data in community studies has its inherent drawbacks : For example, equal emphasis is placed on common and rare species (Lambert and Dale, 1964). In a recent review, Smartt et al. (1974), while accepting the drawbacks of binary data, show that when information on species-environment relations (e.g. species richness, diversity) is required, qualitative (i.e. binary) data are often more suitable than quantitative data.

The index chosen for this study was that described by Czekanowski (1913 ref. in Clifford and Stephenson 1975), and later modified by Sorensen (1948). This index (the Czekanowski Index) is constrained between 0 and 1, which minimises the effect of rare taxa, and its higher values relative to a similarly constrained index - the Jaccard Index - make it more suitable for the purposes of this study.

The formula for calculation of the similarity between two hypothetical sites A and B is given as :

$$\frac{2a}{2a + b + c} \qquad \text{- Czekanowski Index}$$

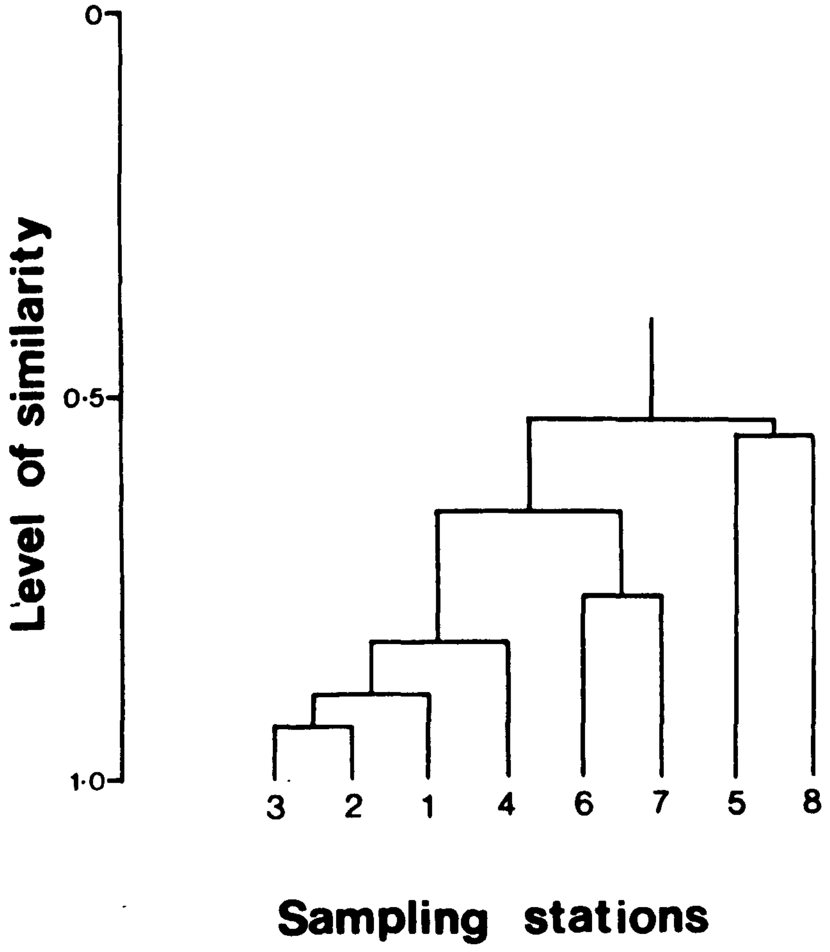
where a = number of shared spp.

b = number of spp. present in A

| 2 | 3 | 4 | 5 | 6 | 7 | 8 | |
|---|---|---|---|---|---|---|---|
| 0.86 | 0.89* | 0.79 | 0.31 | 0.60 | 0.63 | 0.53* | 1 |
| | 0.93* | 0.79 | 0.26 | 0.60 | 0.58 | 0.41 | 2 |
| | | 0.82* | 0.25 | 0.59 | 0.56 | 0.46 | 3 |
| | | | 0.32 | 0.62 | 0.65* | 0.42 | 4 |
| | | | | 0.29 | 0.30 | 0.55* | 5 |
| | | | | | 0.76* | 0.40 | 6 |
| | | | | | | 0.43 | 7 |

TABLE 15 :Coefficients of similarity based on the Czekanowski Index (see text for details), from pooled data given in Tables 7-14, for stations 1-8.

FIGURE 10: Dendrogram linking stations 1-8 according to level of similarity (see Table 15 above) based on the Czekanowski Index.



but absent from B

c = number of spp. present in B

but absent from A.

The Czekanowski indices of similarity between stations 1-8 are given in Table 15; these indices have been calculated from data pooled over the period March 1980 to February 1981. By noting the stations of highest similarity, it is possible to construct a dendrogram (Figure 10), giving a graphic display of the results presented in Table 15. This simple form of clustering the sampling sites according to species composition has effectively separated the downstream (stations 1, 2,3 and 4) and upstream (stations 6 and 7) areas, and has similarly isolated both from the two 'lentic' areas (stations 5 and 8).

(c) site diversity

The relevance of diversity measures as a mathematical tool for examining the structure of biotic communities remains doubtful, despite the argument that diversity is an intrinsic property of such groups (McIntosh 1967). A review of the current status of this debate is given in Green (1980). When applied to lotic communities, whose organisational structure is at best, loose (Reice 1980), diversity measures, which are by definition "attributes of ... natural or organised communities" (Hairston 1964), carry little weight.

However, in this case, the use of diversity measures is for the purpose of augmenting other measures (e.g.

| | | ST.1 | ST.2 | ST.3 | ST.4 | ST.5 | ST.6 | ST.7 | ST.8 |
|---|---|---|---|---|---|---|---|---|---|
| MARCH | : | 0.72 | 0.74 | 0.52 | 0.74 | 0.45 | 0.23 | ** | 0.49 |
| APRIL | : | 0.94 | 0.80 | 0.52 | 0.76 | 0.45 | 0.57 | ** | ** |
| MAY | : | 0.99 | 0.86 | 0.63 | 0.84 | 0.43 | 0.49 | 0.46 | 0.46 |
| JUNE | : | 0.78 | 0.91 | 0.73 | 0.76 | 0.19 | 0.67 | 0.14 | 0.28 |
| JULY | : | 0.80 | 0.79 | 0.87 | 0.17 | 0.61 | 0.76 | 0.62 | ** |
| AUGUST | : | 0.65 | 0.80 | 0.84 | 1.45 | 0.13 | 0.97 | 0.79 | ** |
| SEPTEMBER | : | 0.87 | 0.82 | 0.79 | 0.63 | 0.08 | 0.52 | 0.22 | ** |
| OCTOBER | : | 1.01 | 0.83 | 0.73 | 0.81 | 0.39 | 0.51 | 0.49 | 0.48 |
| NOVEMBER | : | 0.92 | 0.92 | 0.60 | 0.64 | 0.47 | 0.68 | 0.77 | 0.72 |
| DECEMBER | : | 0.98 | 0.94 | 0.82 | 0.82 | 0.16 | 0.57 | ** | ** |
| JANUARY | : | 0.87 | 1.08 | 0.80 | 0.80 | ** | 0.67 | 0.78 | ** |
| FEBRUARY | : | 0.91 | 0.94 | 0.71 | 0.84 | ** | 0.44 | 0.78 | ** |
| MEAN DIVERSITY | : | 0.85 | 0.87 | 0.71 | 0.77 | 0.34 | 0.59 | 0.56 | 0.49 |

TABLE 16 : Shannon Indices of diversity calculated from monthly kick samples for stations 1 - 8 : March 1980 to February 1981

similarity) for purely comparative purposes. In such situations, use of this measure can be justified, and Green (1980) recommends the use of the index S (for definition see below), which although simple, is more biologically valid and less ambiguous than other more complex measures such as H'(for definition see below). In this analysis, both S and H' values are given, but S is recognised to carry more weight.

The index S, which is equivalent to the number of taxa present at each site, has been described by Poole (1974) as "the only truly objective measure of diversity". H', normaly referred to as the Shannon-Weiner index,is more complex, and is based on information theory (Shannon and Weaver 1949). The formula for H' used here is in the form given by Clifford and Stephenson (1975) (although, in this case, logarithms to base 10, not base e, were used):

$$H' = \log_{10}N - 1/N\sum_{1}^{S} n\log_{10}n$$

where: N = grand total of individuals of all taxa at the site,

S = number of taxa,

n = number of individuals in a given taxon.

S values can be obtained from the information given in Tables 7-14; values of H' are given in Table 16. An analysis of variance carried out on the data in Table 16 showed that significant differences existed in values of H' among stations 1-8, particularly between stations 1 and 2 on the downstream area and stations 6-8 on the upstream area. In general, diversity measured as H' was higher in the downstream community than the upstream community throughout most of the study period.

### (d) site differences in species assemblages

#### I : functional feeding groups

Perhaps one of the most important theoretical advances in the biology of stream communities has been the adoption of the concept of 'functional feeding groups' (for a recent review see Cummins and Klug 1979).

In general, this concept has been applied to arthropods, which constitute the dominant phyletic group in the great majority of lotic communities. The central argument is that although most stream macroinvertebrates are catholic in their choice of diet, their feeding mechanisms and digestive strategies tend to favour particular resource types.

Lotic systems tend towards heterotrophy, since total respiration normally exceeds photosynthesis. Allochthonous rather than autochthonous resource input tends to be the major energy source powering stream ecosystems. Allochthonous input is normally derived from the riparian vegetation in the form of leaf litter. The breakdown of leaf litter into processed detrital fractions of various sizes has been well documented (Boling et al. 1975). The availability of these detrital fractions of decreasing size from CPOM (coarse particulate organic matter) to DOM (dissolved organic matter) (definitions in Boling et al. ibid.), together with other, autochthonous forms of resource input (e.g. periphyton, animal tissue) as clearly defined resource types has resulted in niche separation among the various macroinvertebrate species exploiting them. In general, the functional adaptations inherent in efficient exploitation of particular resource types has allowed a number of functional feeding groups to be distinguished.

| | |
|---|---|
| SCRAPERS | grazing on periphyton. |
| COLLECTORS | harvesting bacterially colonised fine particle detritus (e.g.FPOM). |
| SHREDDERS | selecting large particle detritus colonised by fungi/bacteria (e.g.CPOM). |
| PREDATORS | capture live prey. |
| PIERCERS | imbibe cell fluids from pierced macrophyte stems (no sp. of this category were recorded). |

(Definitions from Cummins and Klug 1979)

It is possible, by analysing the relative numbers of each feeding group, to make broad comments on the functional nature of the community studied, e.g. it is possible to predict the nature of the primary resource type.

To classify the species present in the various sampling stations in terms of trophic types with any degree of certainty, it would have been necessary to carry

| TAXA | SCRAPERS | PREDATORS | COLLECTORS | SHREDDERS |
|---|---|---|---|---|
| PLATYHELMINTHES | | | | |
| *Crenobia alpina* | | *** | | |
| OLIGOCHAETA | | | | |
| *Lumbricus terrestris* | | | *** | |
| *Lumbriculid sp.* | | | *** | |
| NEMATOMORPHA | | | | |
| *Gordius sp.* | | DOES NOT FEED AS ADULT | | |
| AMPHIPODA | | | | |
| *Gammarus pulex* | | | | *** |
| ACARINA | | | | |
| Hydracarina | | *** | | |
| ODONATA | | | | |
| *Coenagrion puella* | | *** | | |
| PLECOPTERA | | | | |
| *Brachyptera risi* | (***) | *** | | |
| *Leuctra hippopus* | | | | *** |
| *Amphinemura sulcicollis* | | | | *** |
| *Nemurella picteti* | | | | *** |
| *Isoperla grammatica* | | *** | | |
| *Dinocras cephalotes* | | *** | | |
| *Capnia atra* | | | | *** |
| EPHEMEROPTERA | | | | |
| *Baetis rhodani/muticus* | | | *** | |
| *Rhithrogena semicolorata/germanica* | | | *** | |
| DIPTERA | | | | |
| *Chironomid spp.* | | | *** | |
| *Ceratopogonid spp.* | | | *** | |
| *Simulium sp.* | | | *** | |
| *Dixa sp.* | | | *** | |
| *Tipula/Dicranota spp.* | | | | *** |
| TRICHOPTERA (caseless) | | | | |
| *Diplectrona felix* | | | *** | |
| *Polycentropus flavomaculatus* | | *** | | |
| *Rhyacophila dorsalis* | | *** | | |
| *Philopotamus montanus* | | | *** | |
| TRICHOPTERA (cased) | | | | |
| *Potamophylax cingulatus* | | | | *** |
| *Limnephilid sp.2* | | | | *** |
| *Silo pallipes* | | | | |
| *Goera pilosa* | *** | | | |
| *Arthripsodes sp.* | | | | |
| HEMIPTERA | | | | |
| *Cymatia bonsdorffi* | | *** | | |
| COLEOPTERA | | | | |
| *Elmis aenea*(ADULT) | | | *** | |
| *Elmis aenea*(LARVA) | | | *** | |
| *Dytiscus marginalis*(LARVA) | | *** | | |
| *Gyrinus sp.*(ADULT) | | *** | | |
| MEGALOPTERA | | | | |
| *Sialis lutaria* | | *** | | |
| MOLLUSCA | | | | |
| *Ancylus fluviatilis* | *** | | | |
| *Sphaeriid sp.* | | | *** | |

**TABLE 17 : Macroinvertebrate functional feeding groups: Classification based on Merrit and Cummins (1978), and Cummins and Klug (1978).**

|  | ST.1 |  | ST.2 |  | ST.3 |  | ST.4 |  | ST.5 |  | ST.6 |  | ST.7 |  | ST.8 |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MAR | -- | 19 | -- | 11 | -- | 19 | 7 | 4 | 27 | 10 | -- | -- | NO DATA |  | 16 | 8 |
|  | 62 | 4 | 40 | 10 | 89 | 31 | 2 | 20 | 187 | 572 | 11 | 66 |  |  | 5 | 93 |
| APR | -- | 19 | -- | 7 | -- | 31 | 7 | 5 | 1 | 7 | -- | 6 | NO DATA |  | NO DATA |  |
|  | 40 | 17 | 18 | 8 | 12 | 51 | 18 | 15 | 319 | 819 | 3 | 78 |  |  |  |  |
| MAY | 2 | 34 | -- | 19 | -- | 17 | 3 | 14 | 1 | 1 | 1 | 9 | -- | -- | -- | 1 |
|  | 57 | 25 | 21 | 14 | 4 | 47 | 25 | 25 | 573 | 1213 | 11 | 74 | 2 | 65 | 24 | 175 |
| JUN | -- | 12 | -- | 10 | 1 | 12 | 7 | 1 | -- | 7 | -- | 19 | -- | -- | -- | -- |
|  | 17 | 24 | 11 | 18 | 5 | 24 | 17 | 18 | 66 | 1643 | 7 | 37 | -- | 39 |  | 56 |
| JUL | -- | 8 | -- | 15 | 10 | 13 | 3 | 4 | 3 | -- | -- | 9 | -- | 2 | NO DATA |  |
|  | 20 | 14 | 16 | 15 | 3 | 7 | 26 | 15 | 147 | 156 | 8 | 64 | 7 | 6 |  |  |
| AUG | -- | 3 | 1 | 15 | 2 | 8 | -- | 8 | -- | 5 | 2 | 12 | -- | 1 | NO DATA |  |
|  | 6 | 1 | 42 | 2 | 5 | 22 | 4 | 10 | 17 | 661 | 14 | 25 | 13 | 27 |  |  |
| SEP | 1 | 4 | 2 | 3 | -- | 7 | -- | 2 | 1 | 1 | 1 | 7 | -- | -- | NO DATA |  |
|  | 21 | 5 | 22 | 2 | 5 | 22 | 22 | 15 | 8 | 582 | 7 | 37 | 8 | 111 |  |  |
| OCT | 6 | 9 | 14 | 15 | 14 | 3 | 9 | 3 | -- | 2 | 1 | 15 | -- | 1 | -- | -- |
|  | 21 | 14 | 24 | 11 | 11 | 44 | 5 | 8 | 36 | 181 | 2 | 34 | 11 | 57 | 9 | 24 |
| NOV | -- | 48 | -- | 29 | -- | 47 | -- | 4 | -- | 7 | 6 | -- | -- | 9 | 2 | -- |
|  | 37 | 48 | 24 | 12 | 10 | 10 | 5 | 3 | 91 | 187 | 4 | 6 | 5 | 40 | 3 | 12 |
| DEC | 18 | 18 | 4 | 16 | 17 | 11 | 2 | 3 | -- | 2 | 4 | 2 | NO DATA |  | NO DATA |  |
|  | 30 | 16 | 10 | 4 | 3 | 37 | 8 | 18 | 32 | 561 | 1 | 20 |  |  |  |  |
| JAN | 17 | 9 | 12 | 19 | 3 | 5 | 5 | 9 | NO DATA |  | 2 | 7 | 1 | 2 | NO DATA |  |
|  | 33 | 6 | 31 | 12 | 4 | 14 | 15 | 21 |  |  | 6 | 34 | 33 | 46 |  |  |
| FEB | 21 | 5 | 8 | 14 | 1 | 12 | 4 | 7 | NO DATA |  | -- | 6 | 2 | 3 | NO DATA |  |
|  | 27 | 9 | 7 | 18 | 2 | 14 | 4 | 12 |  |  | 6 | 57 | 2 | 22 |  |  |

|  |  |  |
|---|---|---|
| EACH 'CELL' OF TABLE = | NO. OF SCRAPERS | NO. OF PREDATORS |
|  | NO. OF COLLECTORS | NO. OF SHREDDERS |

TABLE 18: Relative numbers of 'functional feeding group' types in monthly kick samples - see TABLE 17 for species classification

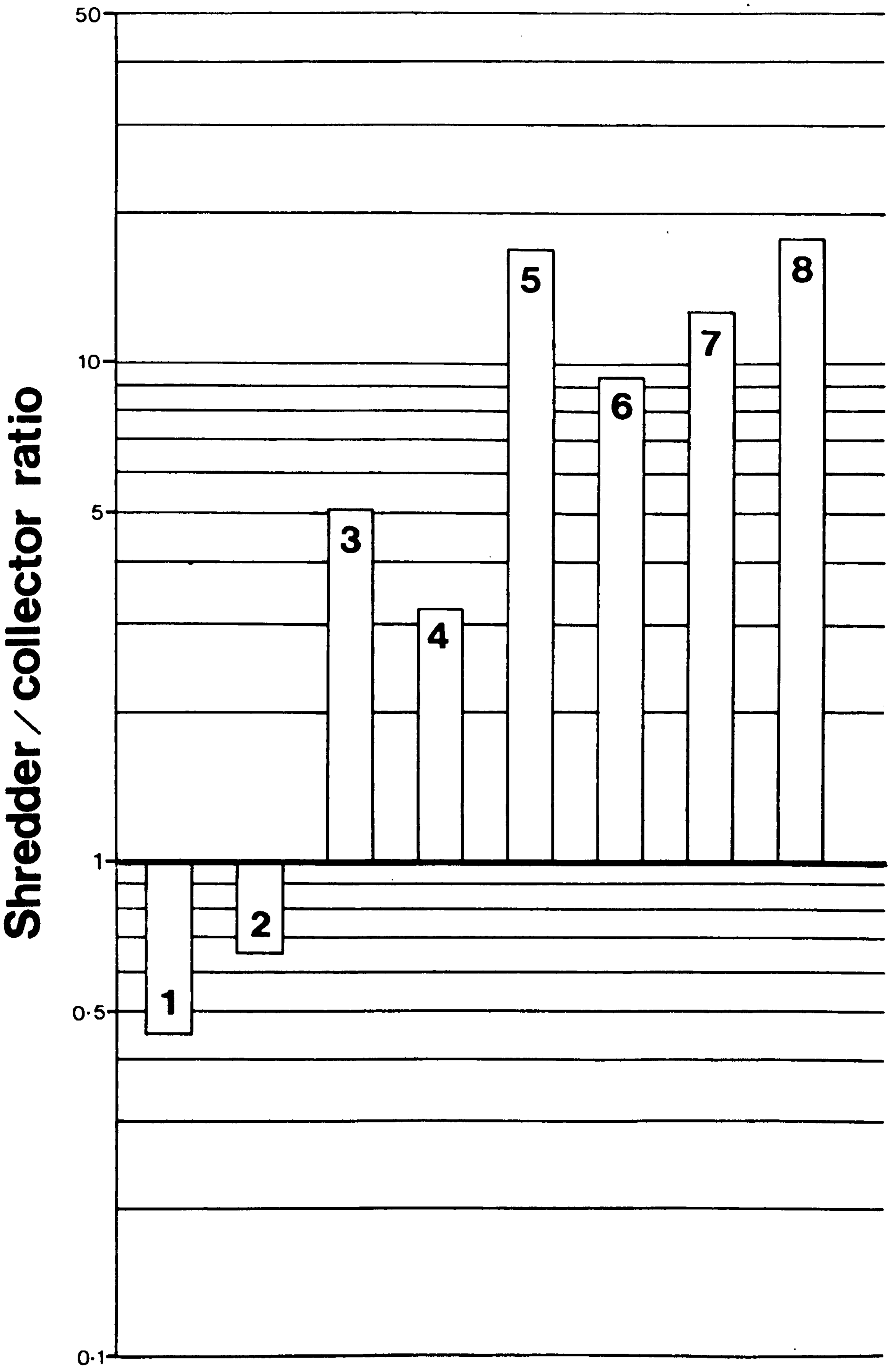
|  | ST.1 | ST.2 | ST.3 | ST.4 | ST.5 | ST.6 | ST.7 | ST.8 |
|---|---|---|---|---|---|---|---|---|
| MARCH | 0.06 | 0.25 | 0.35 | 10.00 | 3.06 | 6.00 | ** | 18.60 |
| APRIL | 0.43 | 0.44 | 4.25 | 0.83 | 2.57 | 26.00 | ** | ** |
| MAY | 0.44 | 0.67 | 11.75 | 1.00 | 2.12 | 6.73 | 32.50 | 7.29 |
| JUNE | 1.41 | 1.64 | 4.80 | 1.06 | 24.89 | 5.29 | D/O | D/O |
| JULY | 0.70 | 0.31 | 2.33 | 0.58 | 1.06 | 8.00 | 0.86 | ** |
| AUGUST | 0.17 | 0.05 | 4.40 | 2.50 | 38.88 | 1.79 | 2.08 | ** |
| SEPTEMBER | 0.24 | 0.09 | 4.40 | 0.68 | 72.75 | 5.29 | 13.88 | ** |
| OCTOBER | 0.67 | 0.46 | 4.00 | 1.60 | 5.03 | 17.00 | 5.18 | 2.67 |
| NOVEMBER | 0.22 | 0.50 | 1.00 | 0.60 | 2.05 | 1.50 | 8.00 | 4.00 |
| DECEMBER | 0.53 | 0.40 | 12.33 | 2.25 | 17.53 | 20.00 | ** | ** |
| JANUARY | 0.18 | 0.39 | 3.50 | 1.40 | ** | 5.67 | 1.39 | ** |
| FEBRUARY | 0.33 | 2.57 | 7.00 | 3.00 | ** | 9.50 | 11.00 | ** |
| MEAN SHREDDER/ COLLECTOR RATIO | 0.45 | 0.65 | 5.01 | 2.21 | 16.99 | 9.40 | 12.65 | 17.71 |

N.B. ** = missing data ; D/O = division by zero.

TABLE 19 :Ratio of ’shredders’ to ’collectors’ in monthly kick samples for stations 1 - 8 : March 1980 to February 1981

<u>FIGURE 11</u>

<u>Ratio of 'shredders' to 'collectors' at stations 1 - 8, calculated from pooled monthly kick sample data.</u>


Shredder / collector ratio
50
10
5
1
0·5
0·1
1
2
3
4
5
6
7
8

out an exhaustive analysis of gut contents. This was clearly outside the scope of this present analysis, and hence species were classified according to the information given in Merritt and Cummins (1978), and Cummins and Klug (1979) for American species. While this renders the assignations of species into functional feeding groups extremely tentative, it was considered that the likelihood of congeneric members of the European fauna exhibiting dietary similarities to their American counterparts was high enough to make this a valid exercise. Where possible, assignations into particular groups were based also on information from European studies. Classification of the 39 taxa identified in this study are given in Table 17. The relative abundances of each group in monthly samples for all eight sites is given in Table 18.

As in the previous two sections, the results show significant structural differences between the upstream and downstream communities. As pointed out by Cummins and Klug (1979), shifts in the relative dominance of the various groups between sites is likely to be indicative of trophic differences. In particular, the shift of the ratio of shredders to collectors towards dominance of shredders in the upstream area, apparent from the results given in Table 19 (summarised in Figure 11), relates directly to the fact that CPOM availability is likely to be higher in the upstream area. This relates to the lower flow rates present in the upstream area, which allow the buildup of leaf 'packs' on the stream bed, from which CPOM is derived.

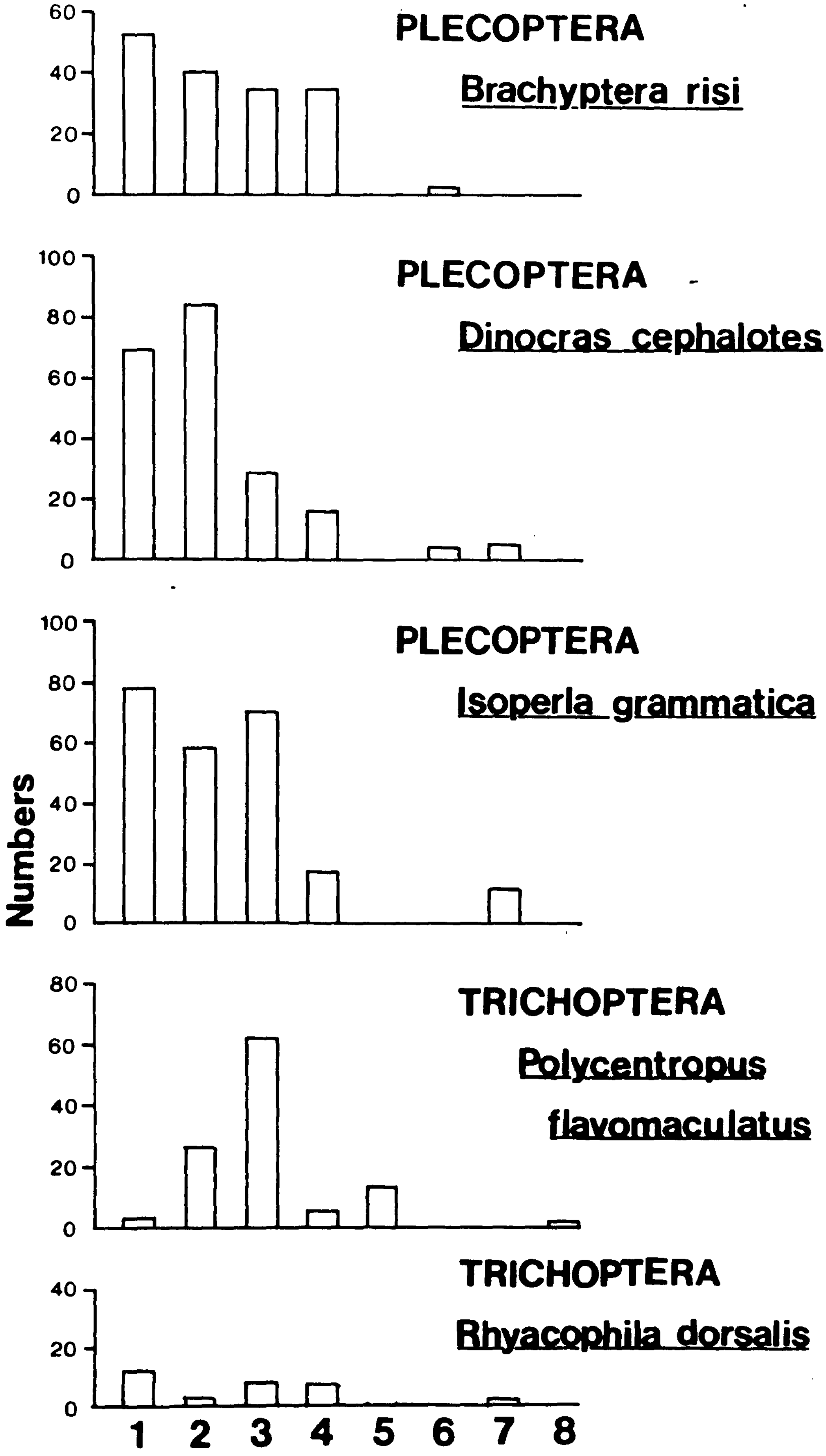
Variations in the number of predator species was also of interest, and is described more fully below. The overall results presented here will be considered in the general discussion.

### (e) site differences in species assemblages
### II : the occurrence of predators of triclads

Observations on lake-dwelling triclad species have tended to suggest that predation is not a major mortality factor in field populations (Davies and Reynoldson 1971). Whether this is also true for stream-dwelling species is less certain, and indeed Wright (1975) has demonstrated that predators may limit the distribution of *C.alpina* populations. In his study, Wright (ibid.) identified four macroinvertebrate species as predators of *C.alpina* by means of serological techniques. Of these four species, three were present in the faunal lists given in Tables 7-14,i.e. *Isoperla grammatica* and *Dinocras cephalotes*, both stonefly larvae and *Rhyacophila dorsalis*, a caseless caddis larva. In addition to these, I have observed two further species feeding directly on triclads in the field: The stonefly larva of *Brachyptera risi* and the caseless caddis larva of *Polycentropus flavomaculatus*. Unfortunately, the positive identification of triclad predators has been based solely on the information given above (but see also Section B of this chapter), since gut squashes of predators yielded no useful information (triclads are completely soft-bodied) and no specific antisera were available for serological analyses. Apart from the direct observations, the evidence presented here

# FIGURE 12

Abundance of five 'predator' species at stations 1 - 8 estimated from pooled kick sample data


PLECOPTERA
Brachyptera risi
60
40
20
0
PLECOPTERA
Dinocras cephalotes
100
80
60
40
20
0
PLECOPTERA
Isoperla grammatica
100
80
60
40
20
0
Numbers
TRICHOPTERA
Polycentropus flavomaculatus
80
60
40
20
0
TRICHOPTERA
Rhyacophila dorsalis
40
20
0
1
2
3
4
5
6
7
8

relies totally on previous results (Wright, ibid.). The pooled abundances of the five 'predator' species are presented in Figure 12, and although differences exist between the downstream area (high abundance) and the upstream area (low abundance) which are consistent for all five species, no positive conclusion can be drawn concerning the relative intensity of predation on triclads. However, simple feeding experiments described in the following Section B showed that all five species fed readily on triclads in the laboratory. However, these results are only of value in a supportative sense, and further analyses are required in order to resolve this situation.

## A(vii) Food Availability

### Introduction

Although freshwater triclads are normally considered as top carnivores, the question still remains as to whether or not stream-dwelling triclad species are active predators. In a recent review, Calow (1980) has pointed out that feeding strategies observed to date in freshwater triclads fall into two categories. The larger species, such as the Dendrocoelidae feed on active prey, to which they are functionally pre-adapted, but incur low metabolic costs in doing so by adopting a 'sit-and-wait' strategy. This contrasts sharply with the smaller species, such as the Planariidae, which are poorly equipped for active predation, and seem to feed on less mobile prey, but by adopting a 'search out'foraging strategy incur higher relative metabolic costs than the larger species. In general, the smaller triclad species tend to be opportunistic feeders, scavenging damaged and disabled prey items. Prey detection is by chemoreception and sensing of tactile stimuli, and thus damaged and struggling animals which leak body fluids are prime sources of stimuli.

In streams, the flow of water through the habitat scours out many animals from the substratum, washing them downstream; this effect is particularly pronounced during periods of spate. Other animals e.g. mayfly larvae may actively leave the stream bed and enter the water current in order to move downstream. Together, these groups of animals respectively form the passive and active components of stream drift. Whether entering the drift deliberately or accidentally, these animals are subject to turbulent forces which are likely to cause them injury or even death. It is these injured or recently dead animals which are likely to fall prey to the scavengers present in the habitat downstream, such as triclads.

In common with the other two typically stream-dwelling triclads found in the British Isles, C.alpina belongs to the family Planariidae. Although no direct studies of foraging strategy have been carried out in this species, there is some evidence to suggest that it conforms to the 'scavenging' type mentioned earlier. Laboratory observations (Baird, unpublished data) suggest that C.alpina will feed readily on any invertebrate with which it is presented, and also that it is reluctant to feed on undamaged prey items. There is also considerable evidence to suggest that C.alpina has a high metabolic rate relative to other triclad species (Whitney 1942; Calow 1977). These findings are highly suggestive of the 'search out' foraging strategy (Calow 1980). It follows that in a stream habitat, C.alpina is likely to derive the bulk of its diet from the drift, since this is the major source of damaged prey items. It seems reasonable, therefore, to measure direct food availability to C.alpina populations in stream habitats by investigating seasonal variations in the quantity of macroinvertebrate drift.

In a recent study, Beveridge (1981) used drift as an index of food availability for a population of Polycelis felina, quoting a paper by Stoneburner and Smock (1979) which indicated the possibility of a direct relationship between drift and benthic density of macroinvertebrates. There is some doubt as to whether such a direct relationship between standing crop and drift exists, particularly when we consider the biasing effects of seasonal downstream migration (Hynes 1970) or 'active drift'. However, for the reasons presented above it seems unnecessary and misleading to invoke such a relationship for the purposes of estimating food availability to stream-dwelling triclads.

## Methods

Two sites were chosen to observe drift over the period April 1981 to March 1982: station 3 on the downstream area and station 6 on the upstream area. Samples were collected from each site simultaneously at approximately monthly intervals. The nets used to collect the samples were wedge shaped, and constructed from coarse zooplankton mesh (pore size approximately 300 μm). Due to the turbulent nature of the habitat, it was necessary to secure the nets inside steel reinforced wire mesh cages in order to prevent movement or dislodgement of the sampler by current flow. The mesh of the cages was sufficient to allow a free flow of water, and did not interfere with the nets inside. The samplers were placed in position flush with the stream bed, in a riffle, and were retrieved 24 hours later. In order to quantify the samples obtained, the amount of water flowing through the net during 24 hours was calculated by the simple formula:

TOTAL WATER                CROSS-SECTIONAL          FLOW
FLOW THROUGH        = AREA OF NET MOUTH   X   RATE   X 86400
NET IN 24 HRS ($m^3$)   SUBMERGED ($m^2$)           ($ms^{-1}$)

A scale was engraved on the mouth of the cage to allow the depth of submergence of the net to be measured easily; this reading, together with flow rate, which was recorded at the mouth of the net with an Ott current meter (three replicate readings), was taken in order to assess changing flow conditions during the sampling period. Following this, samples were removed from the net, placed in polythene containers and returned to the laboratory for analysis. Here, samples were sorted according to the methods given in the previous section. The numbers of each taxa were noted, and the samples were subsequently transferred to a vacuum oven and dried to a constant weight at 45C for 72 hours. After drying, the samples were removed from the oven and weighed on a Mettler microbalance (accuracy ± 0.001 mg.). This was done immediately to minimise the rehydration of samples. In

| TAXA | | | | | 1981 | | | | | | 1982 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | APR | MAY | JUN | JUL | AUG | SEP | OCT | NOV | DEC | JAN | FEB | MAR |
| TRICLADIDA | 0.4 | 0.8 | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | ( 1) | ( 1) | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| OLIGOCHAETA | --- | --- | 3.0 | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | --- | --- | ( 3) | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| NEMATOMORPHA | --- | --- | 114.6 | 7.0 | --- | --- | --- | --- | --- | --- | --- | --- |
| | --- | --- | ( 24) | ( 2) | --- | --- | --- | --- | --- | --- | --- | --- |
| AMPHIPODA | 84.6 | 136.0 | 210.0 | 250.0 | 141.2 | 42.6 | 9.6 | 51.2 | 123.7 | 170.4 | 3.4 | 30.0 |
| | ( 21) | ( 36) | ( 44) | ( 69) | ( 42) | ( 27) | ( 14) | ( 19) | ( 46) | ( 64) | ( 1) | ( 11) |
| PLECOPTERA | 35.6 | 107.0 | 50.0 | 131.6 | 60.9 | --- | 8.4 | 52.2 | 73.4 | 24.1 | 28.8 | 11.3 |
| | ( 37) | (123) | (103) | (314) | (122) | --- | ( 51) | ( 75) | (194) | ( 37) | ( 21) | ( 7) |
| EPHEMEROPTERA | 74.4 | 137.6 | 41.7 | 27.4 | 7.0 | --- | 1.4 | 2.8 | 5.9 | 0.6 | 1.0 | 1.0 |
| | (108) | (153) | ( 79) | ( 57) | ( 24) | --- | ( 4) | ( 15) | ( 33) | ( 3) | ( 3) | ( 3) |
| DIPTERA | 6.4 | 117.6 | 84.8 | 14.4 | 10.8 | --- | 1.0 | 1.2 | 1.1 | 12.9 | --- | --- |
| | ( 7) | ( 12) | ( 5) | ( 26) | ( 22) | --- | ( 4) | ( 1) | ( 3) | ( 18) | --- | --- |
| TRICHOPTERA | 4.8 | 25.7 | 11.2 | 43.0 | 21.6 | 12.4 | 20.4 | 34.6 | 14.4 | 7.2 | --- | --- |
| (CASELESS) | ( 1) | ( 6) | ( 6) | ( 21) | ( 9) | ( 8) | ( 14) | ( 17) | ( 9) | ( 3) | --- | --- |
| TRICHOPTERA | --- | 5.6 | 2.4 | 14.8 | --- | --- | 8.2 | 4.0 | 11.8 | 90.6 | 36.0 | 41.4 |
| (CASED) | --- | ( 3) | ( 3) | ( 2) | --- | --- | ( 2) | ( 1) | ( 3) | ( 11) | ( 4) | ( 2) |
| COLEOPTERA | 5.3 | 18.0 | --- | --- | 1.8 | --- | 3.0 | 1.4 | 0.9 | 20.8 | 1.2 | --- |
| | ( 5) | ( 3) | --- | --- | ( 3) | --- | ( 4) | ( 3) | ( 1) | ( 2) | ( 4) | --- |
| EMERGENT | 7.3 | 14.2 | 39.9 | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| INSECTS | ( 4) | ( 7) | ( 29) | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| TERRESTRIAL | --- | 16.4 | 180.9 | 22.6 | 13.6 | 19.0 | 3.4 | 1.2 | --- | --- | --- | --- |
| INVERTS. | --- | ( 2) | ( 32) | ( 9) | ( 5) | ( 3) | ( 2) | ( 2) | --- | --- | --- | --- |
| TOTAL DRY WEIGHT (mg.) | 218.0 | 578.9 | 738.5 | 510.8 | 256.9 | 74.0 | 55.4 | 148.6 | 231.0 | 326.6 | 70.4 | 83.7 |
| TOTAL NUMBERS IN SAMPLE | (184) | (346) | (328) | (500) | (227) | ( 38) | ( 97) | (133) | (299) | (138) | ( 33) | ( 23) |

000.0 = DRY WEIGHT (mg.)
(000) = NUMBERS
- SEE TEXT FOR DETAILS.

TABLE 20 : Composition of monthly drift samples collected at downstream station 3 over the period April 1981 - March 1982

| TAXA | | | | | 1981 | | | | | | 1982 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | APR | MAY | JUN | JUL | AUG | SEP | OCT | NOV | DEC | JAN | FEB | MAR |
| TRICLADIDA | 1.2 | 2.6 | --- | --- | 0.4 | --- | --- | --- | --- | --- | --- | --- |
| | ( 1) | ( 3) | --- | --- | ( 1) | --- | --- | --- | --- | --- | --- | --- |
| OLIGOCHAETA | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| NEMATOMORPHA | --- | --- | 15.3 | 3.2 | --- | --- | --- | --- | --- | --- | --- | --- |
| | --- | --- | ( 4) | ( 1) | --- | --- | --- | --- | --- | --- | --- | --- |
| AMPHIPODA | 48.6 | 416.4 | 163.4 | 216.4 | 331.8 | 35.6 | 23.2 | 97.8 | 52.7 | 11.4 | 64.6 | 53.8 |
| | ( 27) | (130) | ( 75) | ( 79) | (104) | ( 20) | ( 40) | ( 40) | ( 34) | ( 9) | ( 20) | ( 18) |
| PLECOPTERA | 8.7 | 17.2 | 2.1 | 5.6 | 2.2 | --- | 0.2 | 18.4 | 3.3 | 1.3 | 1.5 | 0.3 |
| | ( 14) | ( 19) | ( 8) | ( 18) | ( 5) | --- | ( 2) | ( 26) | ( 6) | ( 3) | ( 5) | ( 5) |
| EPHEMEROPTERA | --- | 15.8 | --- | 1.6 | --- | --- | --- | 0.2 | 0.8 | --- | 0.3 | 0.2 |
| | --- | ( 22) | --- | ( 4) | --- | --- | --- | ( 2) | ( 2) | --- | ( 1) | ( 2) |
| DIPTERA | 8.3 | 125.6 | 78.9 | 20.4 | --- | --- | --- | 0.8 | 1.2 | 0.4 | 1.2 | --- |
| | ( 1) | ( 8) | ( 7) | ( 4) | --- | --- | --- | ( 3) | ( 2) | ( 2) | ( 3) | --- |
| TRICHOPTERA | --- | --- | 0.5 | 1.2 | --- | --- | --- | 0.4 | --- | --- | --- | --- |
| (CASELESS) | --- | --- | ( 2) | ( 1) | --- | --- | --- | ( 1) | --- | --- | --- | --- |
| TRICHOPTERA | 12.1 | 23.0 | 12.0 | --- | --- | --- | --- | 8.0 | 1.6 | --- | 35.4 | --- |
| (CASED) | ( 16) | ( 28) | ( 5) | --- | --- | --- | --- | ( 3) | ( 1) | --- | ( 14) | --- |
| COLEOPTERA | 0.9 | --- | 0.7 | 1.4 | --- | --- | 1.2 | 4.8 | --- | --- | --- | --- |
| | ( 3) | --- | --- | --- | --- | --- | ( 4) | ( 2) | --- | --- | --- | --- |
| EMERGENT | 1.1 | --- | 0.5 | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| INSECTS | ( 1) | --- | ( 1) | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| TERRESTRIAL | --- | --- | 50.1 | 103.6 | 12.2 | 113.8 | 1.0 | --- | --- | --- | --- | 6.2 |
| INVERTS. | --- | --- | ( 5) | ( 17) | ( 4) | ( 1) | ( 1) | --- | --- | --- | --- | ( 1) |
| TOTAL DRY | | | | | | | | | | | | |
| WEIGHT (mg.) | 80.9 | 600.6 | 323.5 | 353.4 | 346.6 | 149.4 | 25.6 | 130.4 | 59.6 | 13.1 | 103.0 | 60.5 |
| TOTAL NUMBERS | | | | | | | | | | | | |
| IN SAMPLE | ( 63) | (210) | (109) | (126) | (114) | ( 21) | ( 47) | ( 77) | ( 45) | ( 14) | ( 43) | ( 26) |

000.0 = DRY WEIGHT (mg.)
(000) = NUMBERS

TABLE 21 : Composition of monthly drift samples collected at upstream station 6 over the period April 1981 - March 1982

order to minimise bias in sample weight, cased caddis were removed from their cases before drying.

## Results and Preliminary Discussion

Although the total species composition of the drift samples collected from both sites is broadly similar to that obtained from kick samples (see previous section), there were a number of species which were not collected, and one new species which had not been detected by previous sampling. The new species, a nematomorph worm (Gordius sp.) is reputedly semi-aquatic in habit, and is normally found at the extreme edge (i.e. the banks) of the stream habitat, although the larvae are aquatic parasites. There is therefore some doubt as to whether it should be considered as a true member of the stream benthos. Of the species which were previously known to inhabit the benthos at these two areas, but which were not recorded in the drift, or only rarely present, the almost complete absence of C.alpina relative to its density (see following sections) was particularly surprising. The potential significance of this result will be considered in a later section.

No new species were recorded in the drift samples and hence the species list was similar in both stations 3 and 6 to those given in Tables 9 and 12 respectively.

The composition of the monthly drift samples collected at stations 3 and 6 are given in Tables 20 and 21 respectively, and for convenience, species have been grouped into higher taxonomic categories (mainly to order level) and the numbers, dry weights and monthly totals

| | SAMPLE DURATION (hr) | FLOW RATE ($m.s^{-1}$) | TOTAL DISCHARGE ($m^3$) | DRIFT * CONCN.($mg.m^3$) | DRIFT * BIOMASS (mg.) |
|---|---|---|---|---|---|
| APR | 24.0 | 0.43 | 724.5 | 0.45 | 218.8 |
| | (24.0) | (0.36) | ( 489.9) | (0.17) | ( 80.9) |
| MAY | 21.5 | 0.65 | 1358.4 | 0.43 | 646.2 |
| | (21.5) | (0.56) | ( 650.2) | (0.92) | (670.4) |
| JUN | 24.0 | 0.67 | 1563.0 | 0.47 | 738.5 |
| | (24.0) | (0.46) | ( 775.0) | (0.42) | (323.5) |
| JUL | 21.5 | 0.72 | 1170.3 | 0.44 | 570.2 |
| | (21.5) | (0.48) | ( 445.8) | (0.79) | (394.5) |
| AUG | 23.5 | 0.50 | 634.5 | 0.40 | 262.4 |
| | (23.0) | (0.41) | ( 407.4) | (0.85) | (361.7) |
| SEP | 23.0 | 1.13 | 5052.5 | 0.01 | 77.2 |
| | (21.5) | (0.88) | (2452.0) | (0.06) | (166.8) |
| OCT | 24.0 | 1.18 | 1376.4 | 0.04 | 55.4 |
| | (24.0) | (0.78) | (1415.2) | (0.02) | ( 25.6) |
| NOV | 22.8 | 1.58 | 6599.5 | 0.02 | 156.8 |
| | (23.5) | (0.76) | (2121.8) | (0.06) | (133.2) |
| DEC | 26.0 | 0.99 | 2223.9 | 0.10 | 213.2 |
| | (27.0) | (0.27) | ( 275.6) | (0.22) | ( 53.0) |
| JAN | 24.5 | 0.94 | 3233.4 | 0.10 | 319.9 |
| | (25.0) | (0.28) | ( 604.8) | (0.02) | ( 12.6) |
| FEB | 25.5 | 0.92 | 4053.9 | 0.02 | 66.3 |
| | (26.0) | (0.34) | ( 954.7) | (0.11) | ( 95.1) |
| MAR | 25.0 | 0.86 | 3483.0 | 0.02 | 80.4 |
| | (25.5) | (0.86) | (1045.1) | (0.06) | ( 56.9) |

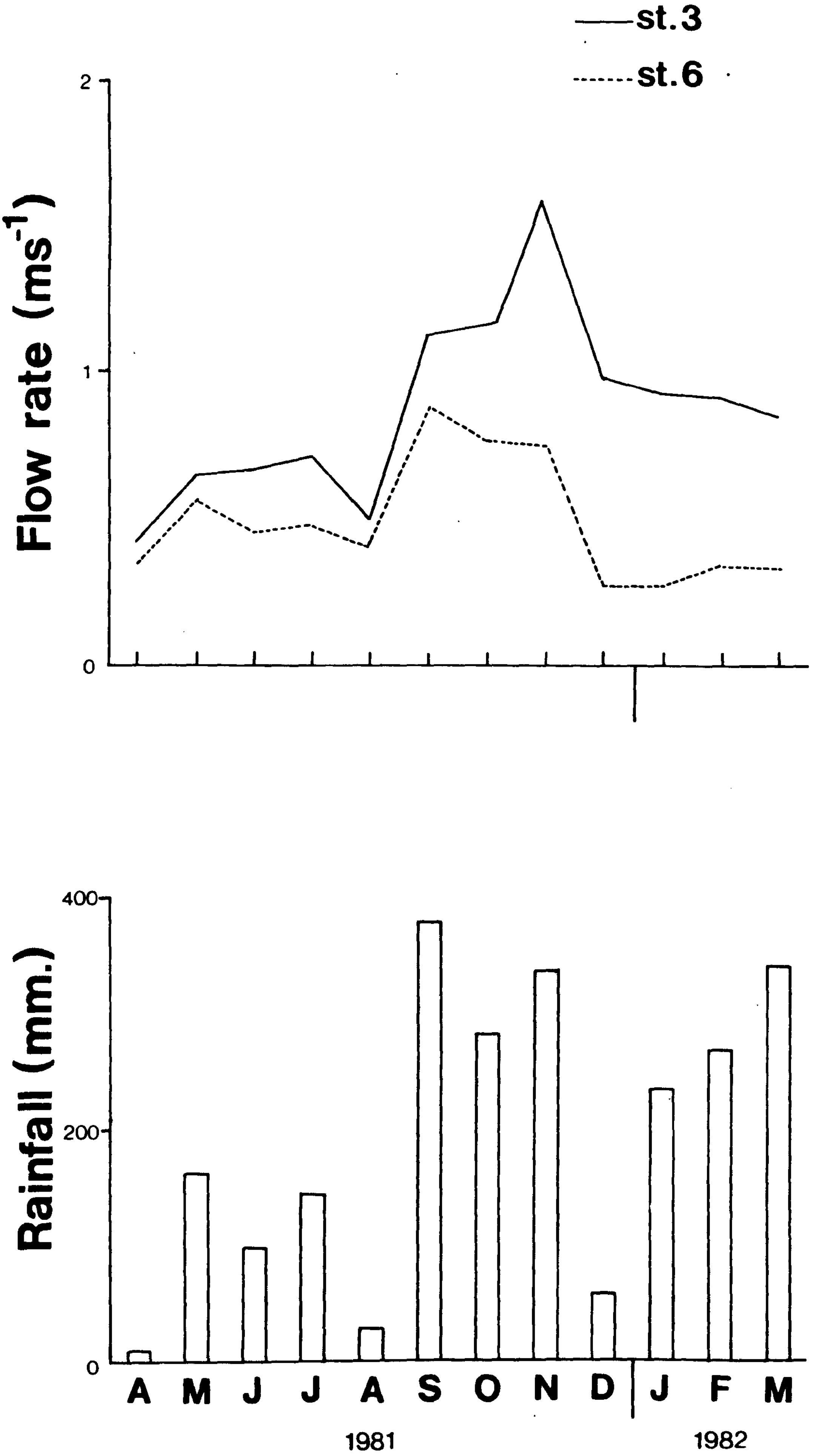
KEY TO TABLE -
0000.0 = RESULTS FROM ST.3
(0000.0)= RESULTS FROM ST.6

TABLE 22 : A summary of the results obtained during the drift measurements at downstream st.3 and upstream st.6 - flow rate, discharge and derived indices (see text).

( * = corrected for standard 24 hr sample.)

# FIGURE 13

Monthly current flow readings recorded at stations 3 and 6, together with monthly rainfall totals (from Table 5) during the period April 1981 to March 1982.

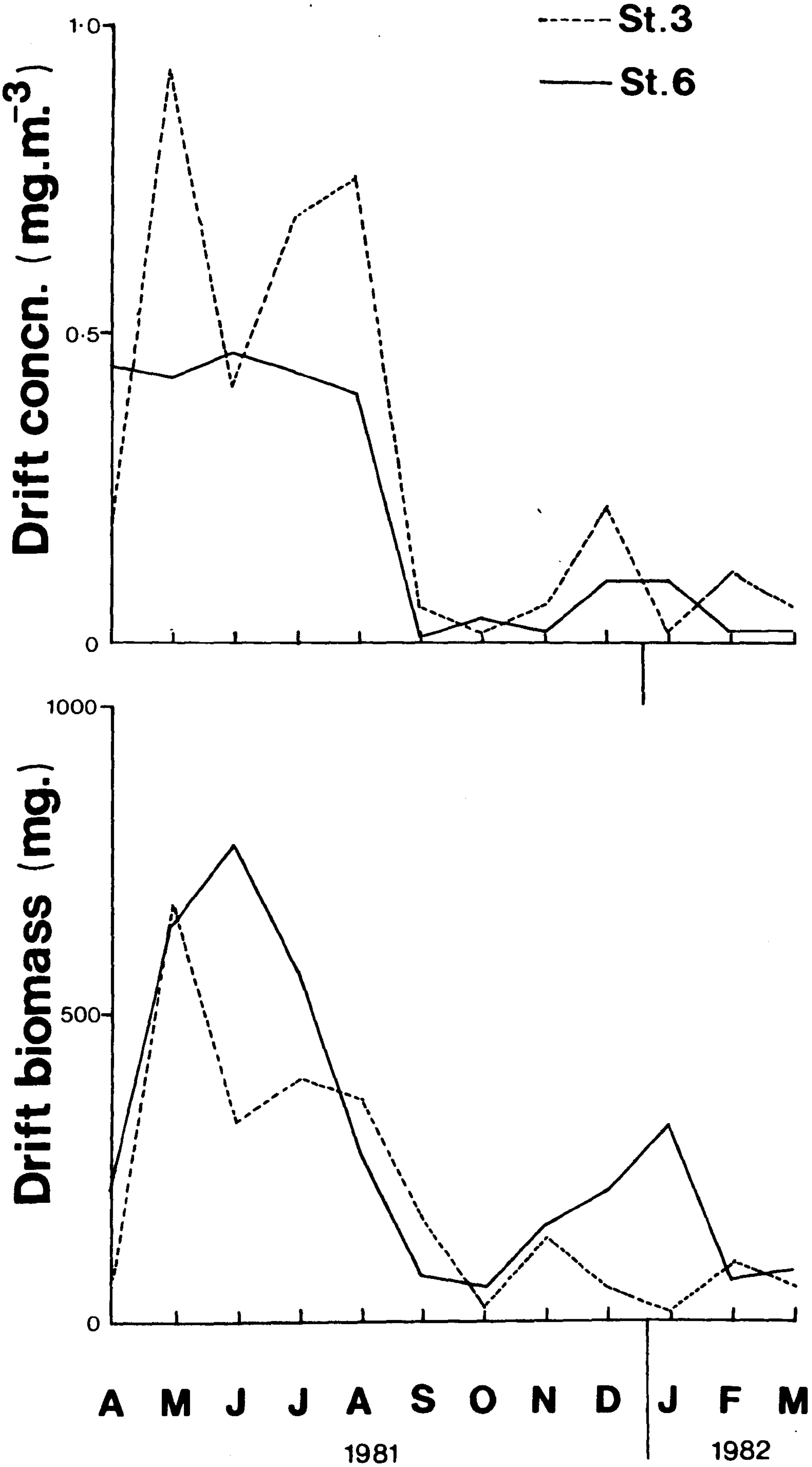

st.3
st.6
Flow rate (ms$^{-1}$)
2
1
0
Rainfall (mm.)
400
200
0
A
M
J
J
A
S
O
N
D
J
F
M
1981
1982

## FIGURE 14

Monthly values of the index of 'drift concentration', measured at stations 3 and 6 during the period April 1981 to March 1982

## FIGURE 15

Monthly values of the index of 'drift biomass', measured at stations 3 and 6 during the period April 1981 to March 1982


St.3
St.6
1·0
0·5
0
Drift concn. (mg.m$^{-3}$)
1000
500
0
Drift biomass (mg.)
A
M
J
J
A
S
O
N
D
J
F
M
1981
1982

given.

From these totals, together with information on sampling time, flow rate and total discharge, two indices have been calculated. The first of these is drift concentration, which represents the total dry weight of drift flowing into the net per cubic metre of discharge. The second, and more important in terms of absolute food availability, is a measure of drift biomass and represents the total dry weight of drift flowing into the net over a 24 hour period. These data, together with the derived indices are presented in Table 22.

If the data on flow rate through the drift nets are examined (Figure 13), it can be seen that the maximum flow readings were obtained for the downstream area from September to December, and for the upstream area from September to November. The flow rates measured at the downstream area were always higher than in the upstream area, especially during the period September to March (maximum flow rate upstream = 0.78 $ms^{-1}$ c.f. 1.58 $ms^{-1}$ downstream).

The index of drift concentration (shown in Figure 14) peaked during spring and summer of the sampling period. During autumn and winter, concentration of drift observed remained low apart from a brief peak in winter (December/January). This pattern was almost identical in both areas. In the upstream area however, drift concentration was more variable, and reached higher levels than in the downstream area (0.17 - 0.92 c.f. 0.40 - 0.47 for station 3). To understand these results however, it is necessary to consider also the pattern of flow during the sampling period and the derived index of drift biomass (see below).

Again, when the index of drift biomass is plotted against time (Figure 15), a pattern of high biomass in spring and summer and low biomass in autumn and winter with a brief minor peak in winter is obtained. The winter peak is less pronounced in the upstream area, but apart from this, the pattern for both areas is broadly similar.

When this index is compared with flow rate, there is a general negative correlation between the two, although this is weaker than that found between flow rate and drift concentration.

The explanation of the spring/summer maxima, and autumn/winter minima in both indices lies not only in a consideration of the period of maximum secondary production in temperate lotic systems, but also in an understanding of the active and passive components of drift.

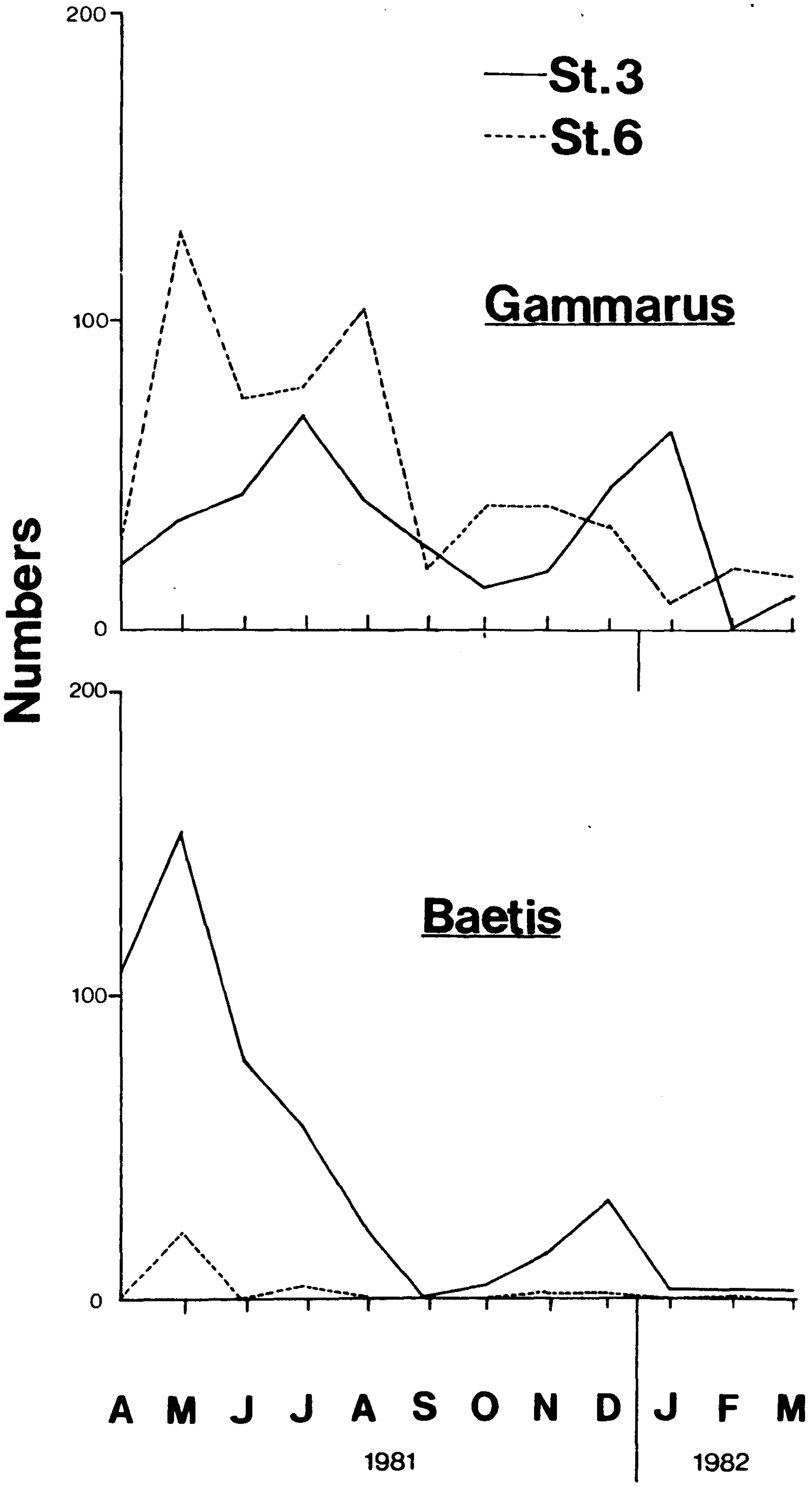
Although the maximum level of secondary production in temperate stream ecosystems normally occurs in spring/summer (Hynes 1970), this also coincides with the maximum level of 'active drift', since this is when competition for space, particularly between insect larvae such as the Ephemeroptera, and emergence occurs. This can be illustrated clearly if the relative numbers of an 'active drifter' (in this case the group "Ephemeroptera" (given in Tables 20 and 21) which was almost completely

## FIGURE 16

Numbers of Gammarus in monthly drift samples at stations 3 and 6 during the period April 1981 to March 1982

## FIGURE 17

Numbers of Baetis in monthly drift samples at stations 3 and 6 during the period April 1981 to March 1982



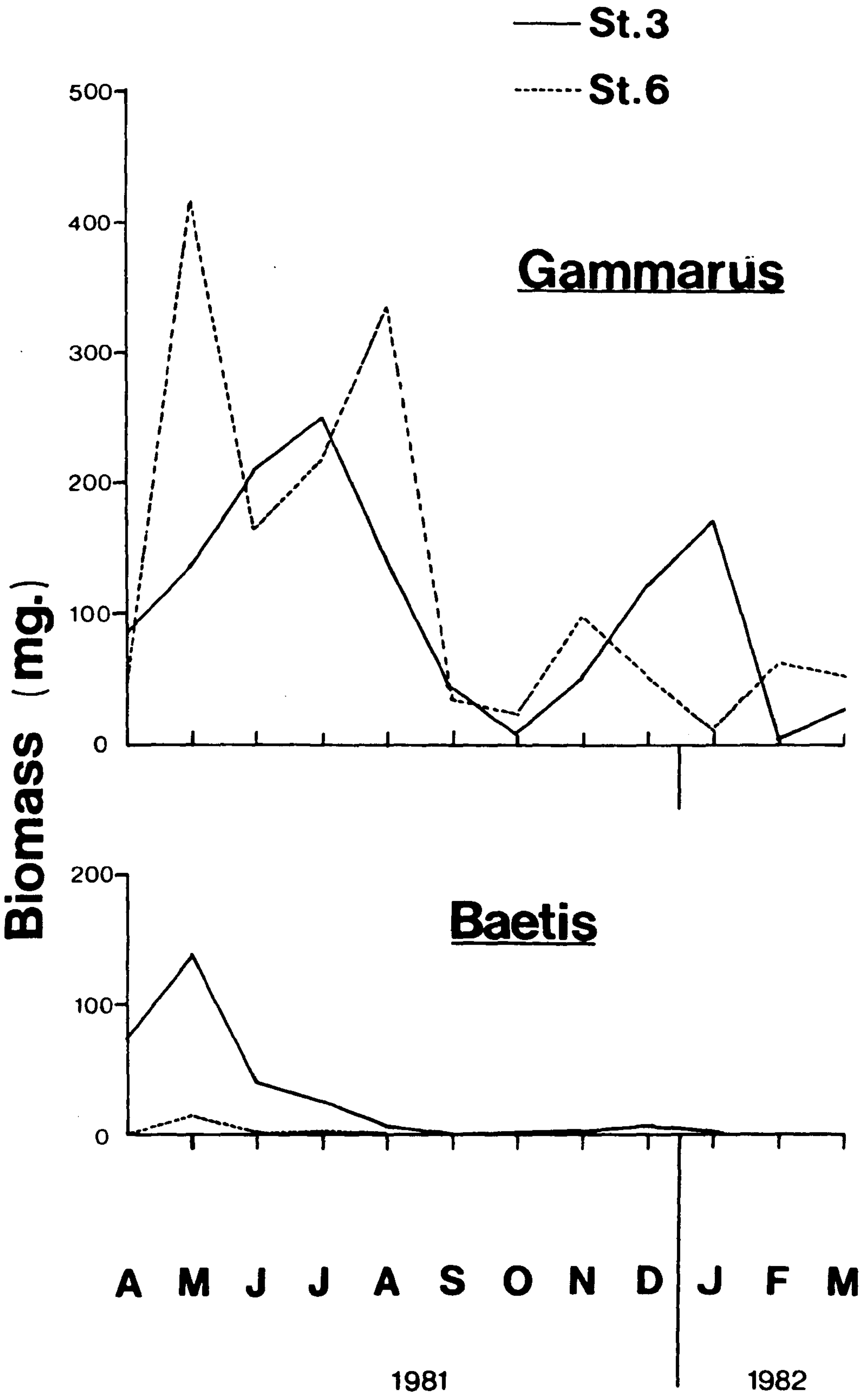
200
St.3
St.6
Gammarus
100
0
Numbers
200
Baetis
100
0
A
M
J
J
A
S
O
N
D
J
F
M
1981
1982

## FIGURE 18

Biomass (mg. dry weight) of Gammarus in monthly drift samples at stations 3 and 6 during the period April 1981 to March 1982

## FIGURE 19

Biomass (mg. dry weight) of Baetis in monthly drift samples at stations 3 and 6 during the period April 1981 to March 1982


St.3
St.6
500
400
300
200
100
0
Gammarus
Biomass (mg.)
200
100
0
Baetis
A M J J A S O N D J F M
1981
1982

composed of nymphs of the species Baetis muticus and B.rhodani) and a 'passive drifter' (in this case the group "Amphipoda" (given in Tables 20 and 21) which consisted entirely of the species Gammarus pulex) are contrasted at both areas over an annual period.

In the case of Gammarus, it can be seen that although the numbers occurring in the drift throughout the year (Figure 16) remain fairly constant (this is less so for the upstream area), the drift biomass of animals follows a clearly bimodal pattern over the year: peaks occur in summer and winter (Figure 18).

The nymphs of Baetis, however, occur in much greater numbers in the drift in spring/summer (Figure 17) and this is reflected in the variation in their drift biomass (Figure 19).

The explanation for these two contrasting patterns is that in spring/summer, Baetis nymphs are ready to emerge, and actively enter the drift. Since they are well adapted to maintaining themselves in situations of high current flow, they are uncommon in the drift at other times of the year. Gammarus populations reach their maximum densities in spring/summer, and at this time, competition for space becomes most severe. Consequently, displaced individuals tend to enter the drift passively, since Gammarus is poorly adapted for life in flowing water habitats, and animals which are forced into sub-optimal areas of the habitat tend to be washed away. Gammarus populations may continue to breed throughout the year, and in autumn/winter, as the flow rate increases, the number of 'safe' sites in the habitat decreases and consequently there is again competition for space resulting in animals being displaced and entering the drift.

The explanation for the bimodal pattern of drift biomass at both sites over the sampling period shown in Figure 15 relates to the increasing influence of current flow as a factor limiting the number of 'safe' sites available to animals poorly adapted for high flow rates, such as *Gammarus*, relative to the decreasing level of the standing crop of benthic macroinvertebrates over the same period. In addition to this, the spring/summer maximum peak also includes large numbers of insect larvae, such as *Baetis* which are undergoing active downstream migration or emergence; in their case, the increasing flow rate over the latter part of the sampling period has little effect. Taken together, these two components of drift result in the bimodal pattern: the major peak being active and passive drift, the minor peak being solely due to passive drift.

Of the two indices calculated, it is the index of drift biomass which is of most interest for the purposes of this study, since it is a direct index of 'total food available to triclads'.

In contrast with the other habitat features described in this section, the index of food availability seem to remain largely similar throughout the study period at both sites. The only major divergence between the two sites occurs in winter: the minor peak in drift biomass is much less obvious in the upstream area than in the downstream area. This seems to be due to the fact, mentioned earlier, that the relative flow rates of the two areas became increasingly divergent towards the end of the study period.

Resource availability is known to have a profound influence on the reproduction of C.alpina in the laboratory (see Section B), and variations existing between the upstream and downstream areas in level of food availability could prove of importance in understanding the differences in the levels of sexual reproduction mentioned in Chapter 1. The implications of this situation receive more detailed consideration in Sections B and C of this chapter.

## Section B : Population Dynamics of C.alpina

### B(i) General Introduction

Although this section presents data on population dynamics, it is primarily concerned with the reproductive ecology of C.alpina: In particular, how population parameters (e.g. density) influence reproduction relative to external factors (see previous section). The data presented here, in common with those in the previous section, were collected over the period March 1980 - February 1982. A discussion of these results follows this section.

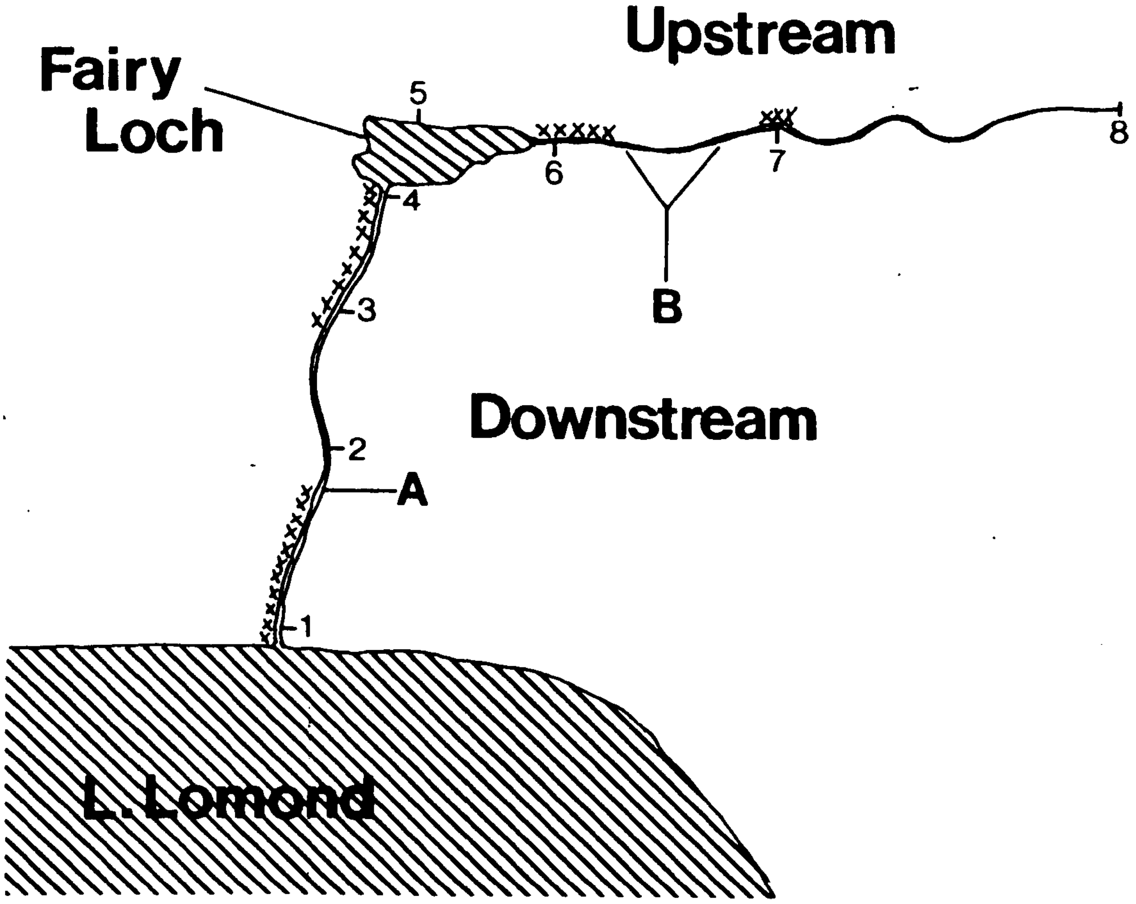
### B(ii) Distribution Within the Study Area

The heterogeneous nature of stream habitats is the result of a number of closely interacting environmental processes. Although these are often complex, the prevailing flow conditions along the length of a stream

# FIGURE 20

Distribution of *C.alpina* in the Fairy Loch system, together with the position of points 'A' and 'B' referred to in section B(ii).

X = *C.alpina* present


Upstream
Fairy Loch
5
6
7
8
4
3
B
Downstream
2
A
1
L. Lomond

are among the most important, influencing many features of the habitat, such as substrate type, temperature and water chemistry.

The occurrence of *C.alpina* in the study area was apparently influenced by the direct and indirect actions of flow rate: directly since *C.alpina* cannot tolerate high flow rates (see below), and indirectly through its effects on substrate particle size.

The distribution of *C.alpina* along the length of the Fairy Loch system was assessed by a continuous sampling of the stream bed from the mouth of the downstream area at station 1 to the source of the upstream area at station 8. A map of this distribution is given in Figure 20.

Triclads were present throughout the study period at five of the eight sampling sites. At the other three sites, no triclads were recorded during this period.

Considering the stream system as a whole, however, the results of the continuous sampling were as follows: in the downstream area, triclads occurred in a continuous pattern from the outflow of the Fairy Loch at station 4 downstream to station 3, and again in a similar pattern from a point below station 2 (marked A on Fig. 20) downstream to the point where the stream entered Loch Lomond immediately below station 1. Triclads were almost completely absent in the area between station 3 and point A, except for a few isolated pockets in areas of quiet flow. This general absence is due to the area of steep gradient which exists between these two points see Fig. 3.

It is probable that the flow conditions in this area effectively act as a barrier to colonisation and upstream dispersal. The limiting actions of high current flow to upstream movement by C.alpina have been convincingly demonstrated in a number of studies (e.g. Wright 1968), and in this case, the gradient between the two points mentioned (see Table 5) lay beyond the upper limit of the tolerance range described for this species (cf.'50%',in Wright 1968).

No triclads were recorded in the area between station 4 and station 6. This area, i.e. the Fairy Loch itself, was basically a lentic habitat. The Fairy Loch 'shore' was steep sided, and was composed of a consolidated mat of sphagnum. There was no littoral region, and hence no suitable substratum existed for colonisation by triclads. The 'mouth' of the upstream area, immediately below station 6, constituted a deposition zone which had been consolidated by Potamogeton beds. Again, the substratum, being entirely composed of silt, was unsuitable for colonisation by triclads. Although silt does not inhibit the locomotory ability of triclads, it renders them highly susceptible to physical disturbance; also, areas of silt may be subjected to periods of low $pO_2$, to which C.alpina is highly intolerant (see Chapter 2).

C.alpina occurred sporadically in the upstream area between station 6 and station 8. In contrast with the erosional nature of the downstream area, the upstream area constituted a depositional system; this could be ascribed to the topography of the area, which resulted in generally low flow rates and hence allowed suspended materials to settle out to form large patches of silt interspersed with 'riffle' areas of gravel and larger stones. These 'riffle' areas constituted the preferred habitat for C.alpina in the upstream area; the larger areas of silt acting as an effective barrier to upstream dispersal.

In general, therefore, the distribution of C.alpina within the study area was limited by the upper and lower extremes of flow rate, with the Fairy Loch itself effectively dividing the study area in two. Any movement between these two 'sub-populations' of C.alpina was likely to be in one direction only, i.e. from the upstream area to the downstream area. This could occur by C.alpina being washed out of the upstream area while attached to buoyant debris e.g. leaves or twigs, although the flow through the Fairy Loch was probably sufficiently slow to make this a rare occurrence.

Movement within the two areas was also likely to be restricted. In the downstream site, the major barrier existed at the steep area around station 2, and any movement of individuals between the upper site (3 and 4) and the lower site (below point A) was likely to be a downstream direction only. In the upstream area, movement of individuals between sites was more difficult to assess, although it seemed likely that the larger area of silty bottom e.g. at point B between stations 6 and 7 (see Fig. 20) would present a formidable obstacle to upstream movement by triclads. It is probable, however, that some movement of individuals between sites occurs in the region, although this was likely to be in a predominantly downstream direction.

## B(iii) Population Density Estimates

Previous studies on freshwater triclads have employed a variety of techniques to estimate population size. The most commonly used method is currently that described in Reynoldson (1958), in which population size is estimated by the number of triclads collected during one hour by hand sampling. It was considered that this technique was largely unsuitable for this study for a number of reasons:

(i) Sampling efficiency was likely to be influenced by conditions which influence the sampler (e.g. weather).

(ii) The time required to collect such samples was prohibitive, relative to the value of the data obtained.

(iii) Physical removal of large numbers of animals from the substratum would cause considerable disturbance, even if carefully replaced after counting. It was decided to avoid this where possible.

(iv) The timed sampling method of estimating population size is not a truly quantitative technique. Statistical measures of sampling error are not possible.

Other wider criticisms can also be made: Comparability of results between studies carried out at different locations by different people is questionable. A more quantitative technique was therefore required.

Techniques for estimating the density of benthic macroinvertebrates are usually a trade-off between feasibility of implementation and accuracy of estimation. The relative merits of a variety of techniques have been discussed by Macan (1958) and Calow (1972). For reasons mentioned above, time-limited techniques, together with those in which collection involves excessive disturbance of the habitat, have been rejected for the purposes of this study. Also rejected, for reasons of their dubious connections with reality (Crossmann and Cairns 1974), are those involving the use of artificial substrates. One remaining approach, used initially by Schrader (1932), involves removing stones at random from the habitat and counting the number of organisms on each. However, the main difficulty of this technique is calculating the area of the stone being sampled. A technique proposed by Calow (1972), and based on a modification of Schrader's technique overcomes this problem by obtaining a relationship between stone surface area and the product of its largest perimeter and longest length. Unfortunately this relationship must be recalculated for each new habitat studied, and the method for doing this is tedious. The approach used here is based on his rationale, but sacrifices some of the precision for simplicity, to yield data which are ecologically meaningful.

The individual stones in the substratum of a stream bed constitute the minimum sampling unit available for this study. As Elliott (1977b) states, choosing the smallest possible sampling unit to make up a sample conveys inherent statistical advantages. However, there are two initial problems involved in taking this approach: Firstly, if the numbers of animals (in this case, triclads) on each stone are to be counted correctly, accurate identification of the species being sampled is crucial i.e. it must be visually distinguishable in situ from other species of similar appearance. Secondly, the stones on the bed of a stream come in a variety of sizes i.e. they vary in surface area; this must be taken into account in obtaining the density estimate. Fortunately, initial sampling of the habitat prior to the initiation of the sampling program showed that only one species of triclad (C.alpina) was present in the study area, and therefore no problem existed concerning its correct identification. One further observation made during preliminary sampling was that C.alpina only occupied the bottom areas of stones collected, possibly to avoid exposure to direct sunlight (Beauchamp 1937). Thus in obtaining a density estimate, it was only necessary to relate numbers of animals observed to the undersurface area of the stones being sampled. Stones present were divided into a number of size classes, relating to undersurface area. This was done by comparing each stone with a standard template.

Four class intervals were used: 0-25 $cm^2$ , 25-50 $cm^2$ , 50-100 $cm^2$ and 100-300 $cm^2$ . Preliminary sampling suggested that stones <5 $cm^2$ did not bear triclads, and were threfore ignored during sampling. Stones >300 $cm^2$ were rare at all stations, and were similarly ignored. Stratified random samples were taken at each site to reduce the error due to over- or underestimation of undersurface area. Five replicates of each stratified sample were taken at each of the five stations, where triclads occurred (see previous section) throughout the first year of study from March 1980 to January 1981.

| stone size-classes | SAMPLING STATIONS | | | | |
|---|---|---|---|---|---|
| | 1 | 3 | 4 | 6 | 7 |
| 0 - 25cm$^2$ | 93.0 | 102.3 | 186.0 | 66.5 | 74.0 |
| 25 - 50cm$^2$ | 87.0 | 77.8 | 128.0 | 40.5 | 57.0 |
| 50 - 100cm$^2$ | 18.7 | 16.0 | 9.3 | 14.4 | 15.0 |
| 100 - 300cm$^2$ | 15.0 | 10.0 | 4.3 | 7.5 | 7.0 |

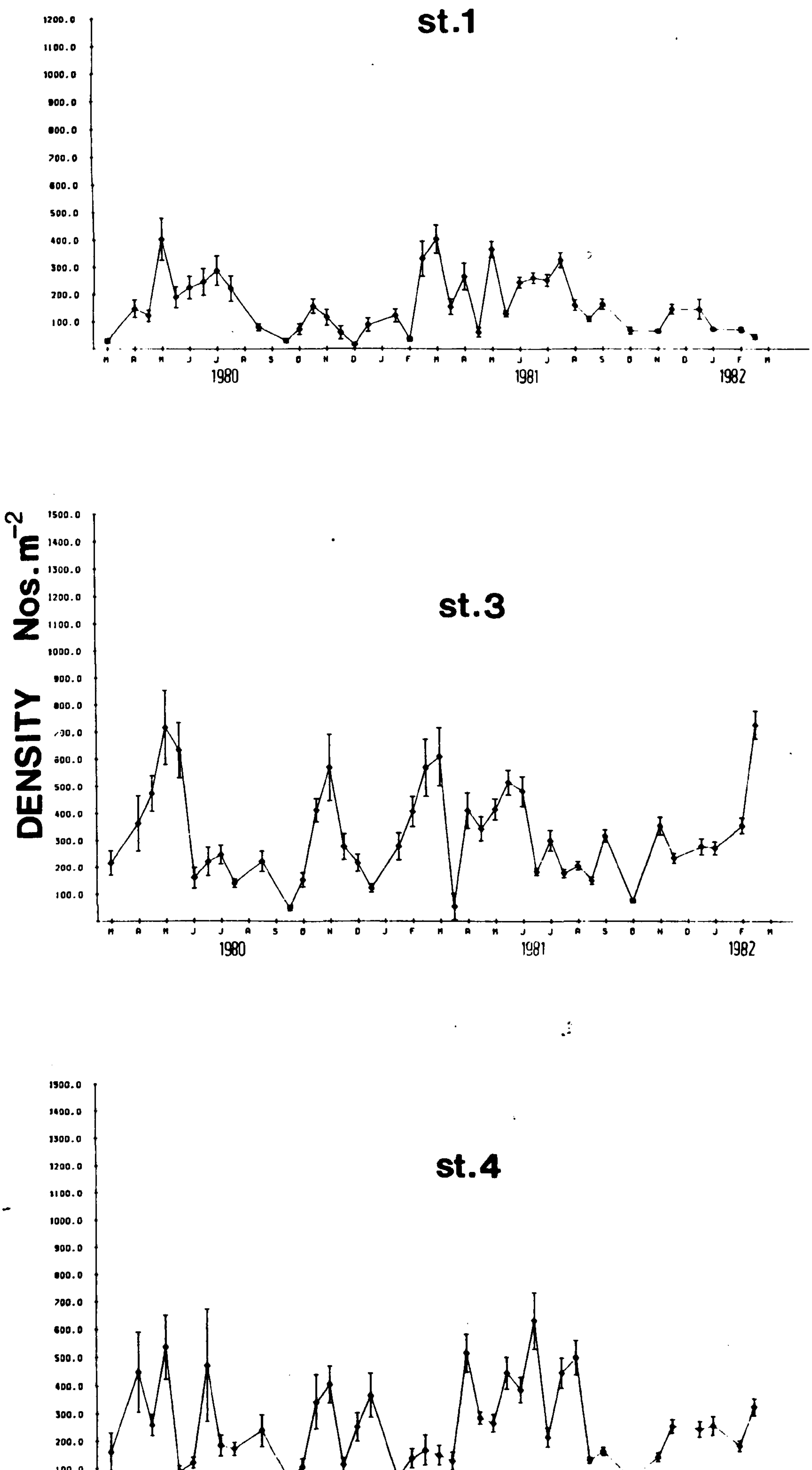
Table 23 : Relative abundance (population $\mu$) values for the four stone size-classes chosen - (numbers per m$^2$ of stream bottom), used as weighting factors ($y_1$-$y_4$) - see text.

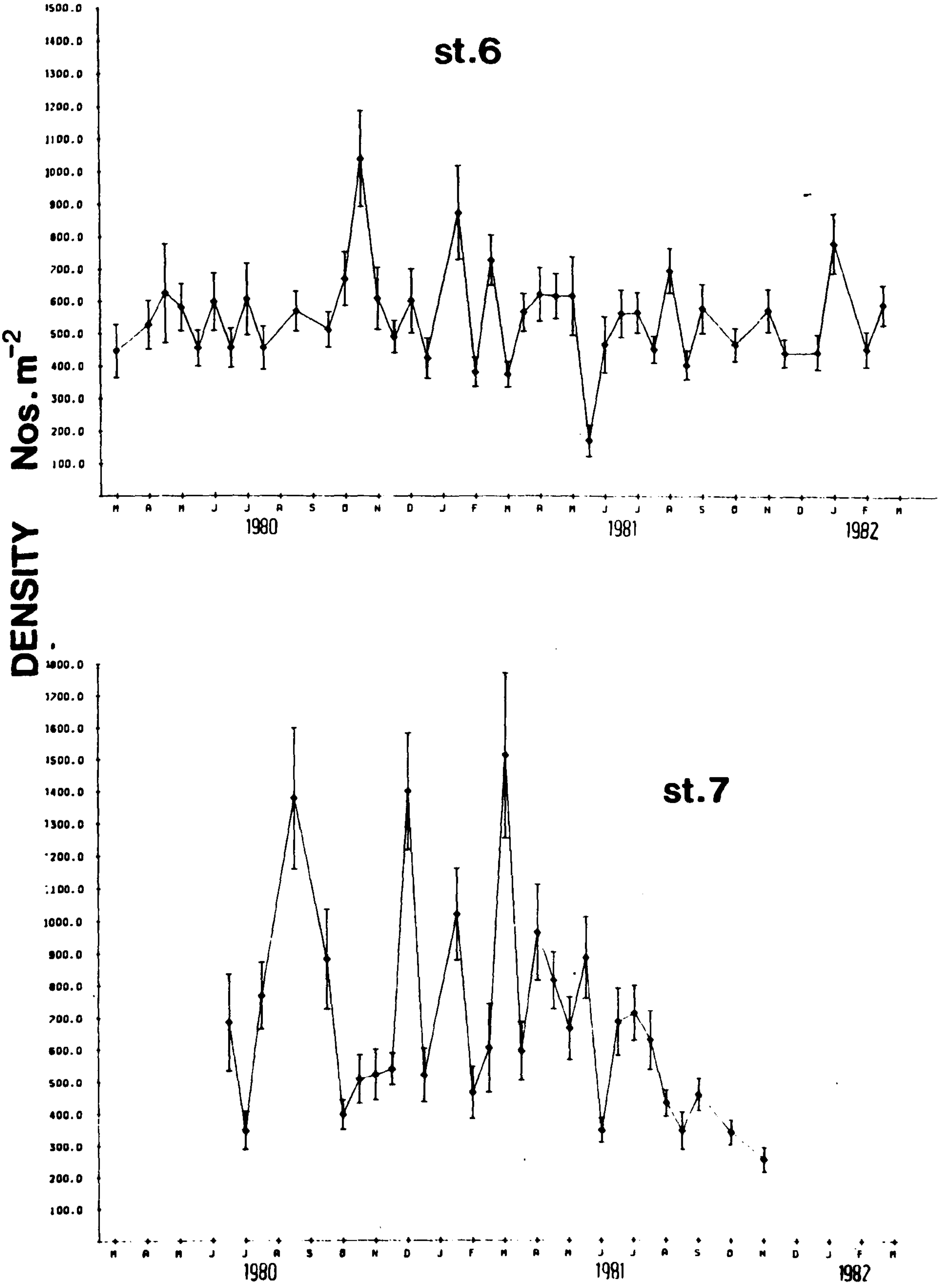
Following evaluation of these data, the number of replicates taken at stations 1,3 and 4 was increased to ten in order to reduce sampling error. Total sample size for stations 6 and 7 was therefore n=20 throughout the study period, whereas at stations 1,3 and 4 it was n=20 from March 1980 to January 1981 and n=40 from February 1981 to February 1982. Samples were obtained at fortnightly intervals throughout the period March 1980 to February 1982. Density estimates were calculated as follows: Mean numbers of triclads per stone were calculated for each size category of stone included in the sample (in this case, the four size categories 0-25, 25-50, 50-100 and 100-300 had respective mean values $\bar{x}_1$ ,$\bar{x}_2$ ,$\bar{x}_3$ and $\bar{x}_4$). To correct for the relative abundance of size categories of stone, each mean had to be multiplied by a corresponding weighting factor. Weighting factors ($y_1$ -$y_4$) were obtained by counting the number of each size category of stone present in the substrate by means of 1m quadrats. Due to the small size of the sampling stations, it was possible to count all the stones present at each, and thus an accurate measure, rather than an estimate, of the relative numbers was obtained. Weighting factors for each site were calculated separately, and are presented in Table 23. In order that the habitat at all stations remained undisturbed before and during the sampling period, these measurements were carried out after sampling had been completed (i.e. March 1982).

It was assumed that the relative numbers of each size category of stone at each site remained constant throughout the sampling period i.e. although some

# FIGURE 21

Population density estimates (±95% confidence limits) collected at roughly fortnightly intervals at stations 1,3,4,6 and 7 over the period March 1980 to February 1981


st.1
1200.0
1100.0
1000.0
900.0
800.0
700.0
600.0
500.0
400.0
300.0
200.0
100.0
M A M J J A S O N D J F M A M J J A S O N D J F M
1980
1981
1982
DENSITY Nos.m$^{-2}$
st.3
1500.0
1400.0
1300.0
1200.0
1100.0
1000.0
900.0
800.0
700.0
600.0
500.0
400.0
300.0
200.0
100.0
M A M J J A S O N D J F M A M J J A S O N D J F M
1980
1981
1982
st.4
1500.0
1400.0
1300.0
1200.0
1100.0
1000.0
900.0
800.0
700.0
600.0
500.0
400.0
300.0
200.0
100.0
M A M J J A S O N D J F M A M J J A S O N D J F M
1980
1981
1982


st.6
st.7
DENSITY Nos. m$^{-2}$
1500.0
1400.0
1300.0
1200.0
1100.0
1000.0
900.0
800.0
700.0
600.0
500.0
400.0
300.0
200.0
100.0
1800.0
1700.0
1600.0
M A M J J A S O N D J F M A M J J A S O N D J F M
1980
1981
1982

downstream movement of substrate probably occurred, immigration balanced emigration at all stations. Having obtained accurate measures of the weighting factors, density was estimated according to the simple formula:

$$\text{Density (nos.m}^{-2}\text{)} = \bar{x}_1 y_1 + \bar{x}_2 y_2 + \bar{x}_3 y_3 + \bar{x}_4 y_4$$
$$= \sum_{1}^{n} x_n y_n$$

Variance estimates were obtained for each sample according to the formula:

$$V(\bar{x}_1 y_1 + \bar{x}_2 y_2 + \bar{x}_3 y_3 + \bar{x}_4 y_4) = (V(\bar{x}_1).y_1^2) + (V(\bar{x}_2).y_2^2) + (V(\bar{x}_3).y_3^2) + (V(\bar{x}_4).y_4^2)$$

In this case, $V(\bar{x}_i) = \frac{s^2}{n_i}$

where $n_i$ = no. of stones in the $i$th stratum

95% confidence limits were calculated by the formula:

$$95\%\text{C.L.} = t_{P=0.05} \times s \quad (s = \text{standard error})$$

where $s = \sqrt{V(\bar{x}_1 y_1 + \bar{x}_2 y_2 + \bar{x}_3 y_3 + \bar{x}_4 y_4)}$

A worked example using these formulae is given in Appendix 1.

The density estimates obtained at all five stations over the period March 1980 to February 1982, together with 95% confidence limits, are presented in Appendix 2. These data are summarised for each station in Figure 21.

Before considering these results in detail, it is necessary to point out that the estimates of density obtained at site 7 during the period March 1981 to November 1981 were greatly influenced by artificial conditions induced as part of an experiment which is considered in the following Section(C). These data receive no further consideration in this section.

|  | SAMPLING STATIONS |  |  |  |  |
|---|---|---|---|---|---|
|  | 1 | 3 | 4 | 6 | 7 |
| Grand x Density<br>±95% C.L. | 161<br>±34 | 328<br>±55 | 250<br>±48 | 552<br>±44 | 758<br>±283 |
| No. of Samples | 40 | 40 | 40 | 40 | 16 |
| Microhabitat Area $m^{-2}$ Bottom Area | 0.883 | 0.740 | 0.868 | 0.493 | 0.559 |
| 'Corrected' Grand $\bar{x}$ Density | 182 | 443 | 288 | 1120 | 1356 |

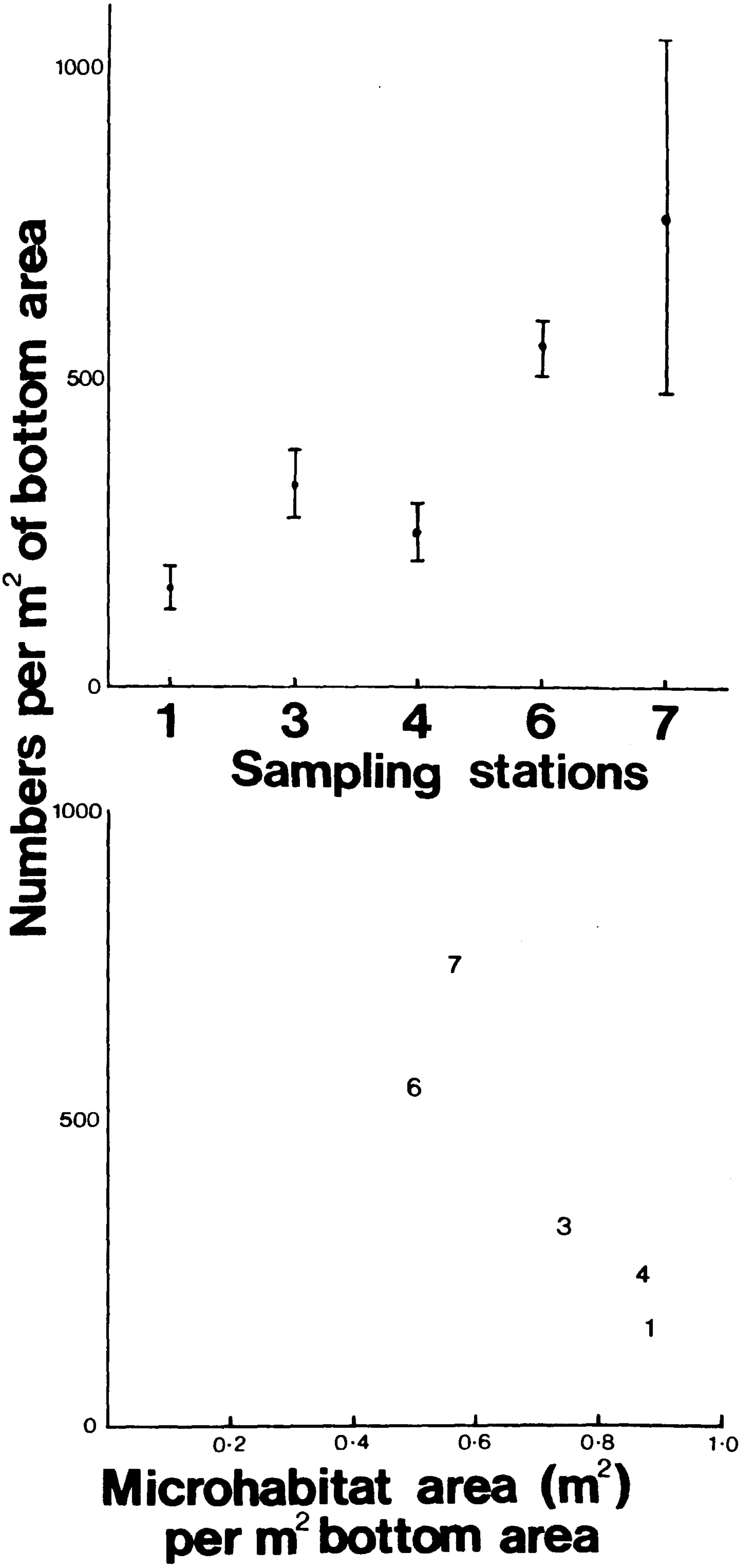
Table 24 : Density statistics obtained from the data in Appendix 2, together with information on microhabitat - for an explanation see text.

## FIGURE 22

Grand mean ($\bar{X}$) density (±95% confidence limits) at stations 1,3,4,6 and 7, calculated from data pooled over the period March 1980 to February 1982 (N.B. data for station 7 excludes estimates obtained after February 1981).

## FIGURE 23

Grand mean ($\bar{X}$) density versus microhabitat area (= undersurface area) per $m^2$ of bottom area for stations 1,3,4,6 and 7.



Numbers per m² of bottom area
1000
500
0
1
3
4
6
7
Sampling stations
1000
500
0
7
6
3
4
1
0·2
0·4
0·6
0·8
1·0
Microhabitat area (m²)
per m² bottom area

The results presented in Appendix 2 reflect considerable variation in population size between sampling stations throughout the study area. By pooling the data for each station, and calculating grand means (together with 95% confidence limits) as given in Table 24, these differences can be clearly distinguished. When these data are summarised (Figure 22), it can be seen that the downstream stations (1,3, and 4) cluster together at density levels of a much lower magnitude than the upstream stations (6 and 7).

Since the estimates of density are calculated in terms of numbers $m^{-2}$ of stream bed, the difference between the upstream and downstream areas may reflect the relative availability of preferred triclad microhabitat e.g. $m^2$ of stone undersurface area in the stream bed at each station. In order to test this possibility, the relative availability of stone undersurface area $m^{-2}$ was estimated for each station. To do this it was assumed that the average stone surface area in each size class was approximately equal to the middle of the class interval. Thus:

0 – 25 $cm^2$ : 12.5 $cm^2$ $= A_1$

25 – 50 $cm^2$ : 37.5 $cm^2$ $= A_2$

50 – 100 $cm^2$ : 75.0 $cm^2$ $= A_3$

100 – 300 $cm^2$ : 200.0 $cm^2$ $= A_4$

By multiplying each median value ($A_n$) by the appropriate relative abundance of stones ($y_1 - y_4$ : defined earlier) at each station, an estimate of microhabitat area m can be obtained from:

$$\text{Total undersurface area m}^{-2}\text{ bottom} = (12.5y_1) + (37.5y_2) + (75y_3) + (200y_4)$$

These are presented for each station in Table 24.

If the generally higher densities found at the upstream stations (6 and 7) relative to the downstream stations (1, 3 and 4) did reflect a greater availability of preferred microhabitat, a positive correlation would be predicted between triclad density (in terms of numbers m stream bed) and total available surface area (m stream bed). In fact, as shown in Figure 23, a negative correlation between these two variables exists over the five stations sampled, and therefore this possibility can be rejected.

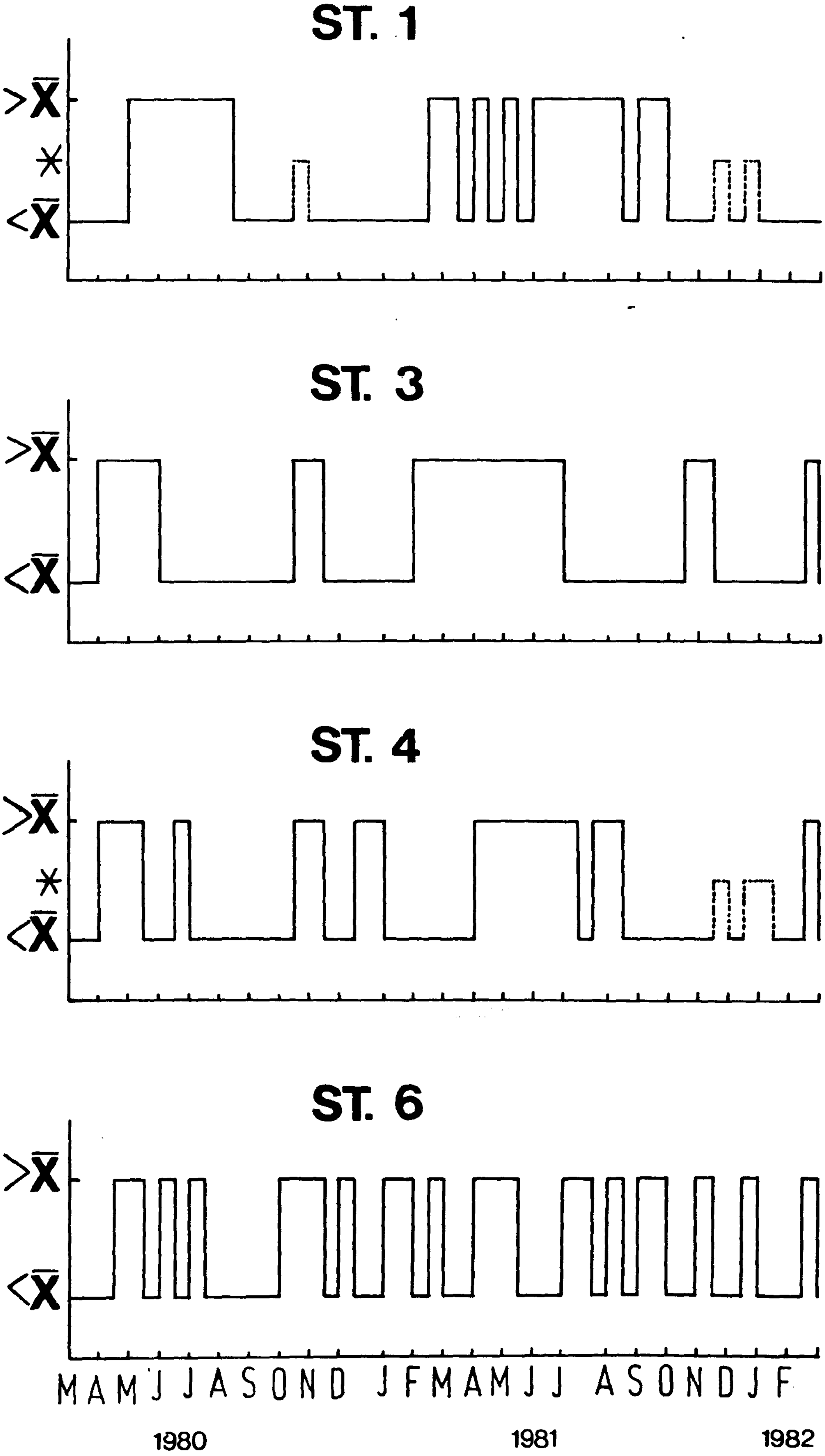
Indeed, when the grand mean densities given in Table 24 are corrected to produce rough estimates of triclad numbers $m^{-2}$ of stone undersurface area, the differences between the upstream area (stations 6 and 7) and the downstream area (stations 1,3, and 4) become even more distinct (values given in Table 25).

Clearly the method used to estimate total undersurface area has been crude; and the adoption of this term as a measure of the preferred microhabitat of triclads is an oversimplification (microhabitat preference undoubtedly reflects the interaction of a number of other factors e.g. food availability, flow rate etc.). Despite these problems, however, it seems likely that the level of variation in average population size reflects real differences between the upstream and downstream areas, the causes of which are discussed in the following chapter.

## FIGURE 24

Density estimates from Appendix 2 for stations 1,3,4, 6 and 7, scored on whether or not they exceeded respective grand mean ($\bar{X}$) values given in Table 25.

* indicates a value just below $\bar{X}$ (see text)


ST. 1
$>\bar{X}$
*
$<\bar{X}$
ST. 3
$>\bar{X}$
$<\bar{X}$
ST. 4
$>\bar{X}$
*
$<\bar{X}$
ST. 6
$>\bar{X}$
$<\bar{X}$
M A M J J A S O N D J F M A M J J A S O N D J F
1980
1981
1982

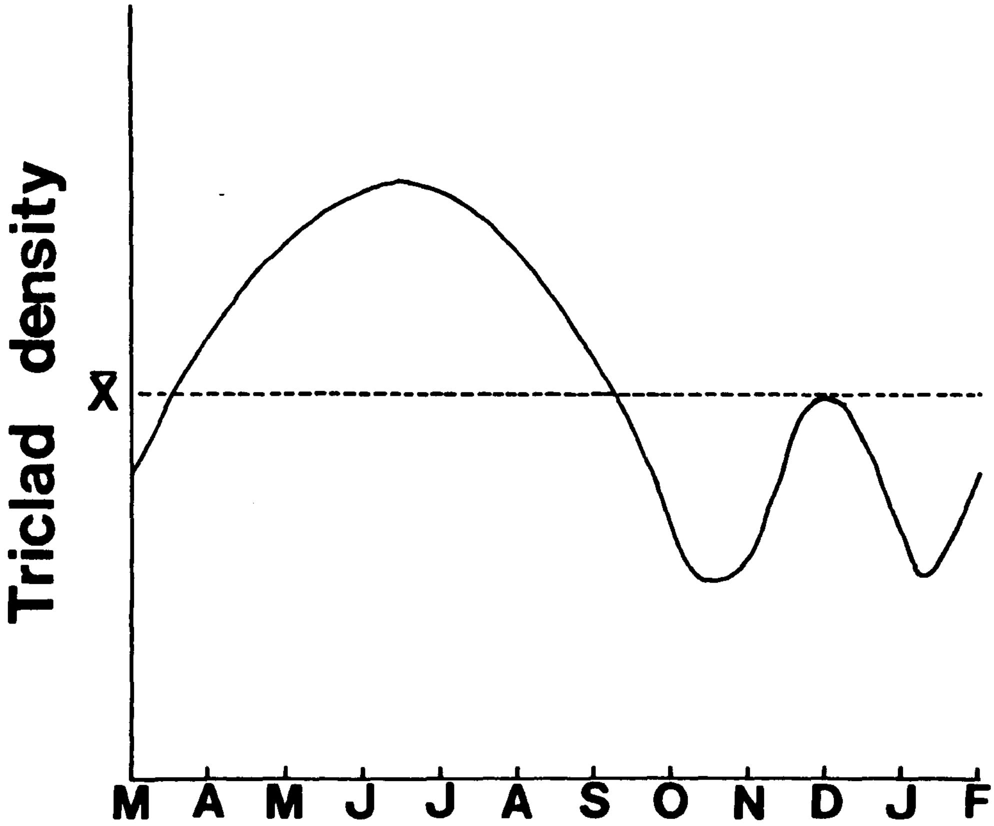
Unlike between-station variation in density, variation in density within each individual station throughout the sampling period has proved difficult to interpret. Due to the necessarily short duration of the sampling period (2 years) formal time-series analysis was considered to be inappropriate for detecting seasonal trends. Instead, this has been attempted by examination of the densities given in Fig. 21, and by assessing peaks and troughs by an arbitrary method described below.

A visual examination of the data for the upstream stations 6 and 7 (Fig.21) suggests, particularly at station 6, that there is little evidence for any seasonal trends or fluctuations in density in the upstream area. Admittedly station 7 exhibits high fluctuations in density, but these tend to be unpredictable in their occurrence, and probably reflect problems inherent in sampling a group of animals which inhabit an extremely restricted (in terms of substrate availability) habitat at high density.

In marked contrast to the upstream area , stations in the downstream area (1, 3 and 4) showed distinct seasonal fluctuations in population size which were generally similar in nature. This can be seen clearly in Figure 24, where the densities collected during the period March 1980 to February 1982 were scored on whether or not they exceeded the grand mean values (given in Table 24). This was carried out for each of the downstream stations (1,3 and 4), and a similar plot for upstream station 6 was provided for comparative purposes. In general, density

FIGURE 25

Hypothetical plot of density versus time for a 'typical' downstream station.


Triclad density
X̄
M
A
M
J
J
A
S
O
N
D
J
F

increased in the downstream stations in late spring, to reach a maximum value in summer followed by a decline in late summer and a lesser peak in late autumn/early winter. In stations 1 and 4, these lesser autumn/winter peaks did not always exceed the grand mean, but could be detected, and are indicated as '*' in Fig. 24.This annual cycle in population density exhibited by the downstream stations is summarised in Figure 25. In contrast, the similar plot (in Fig. 24) given for upstream station 6 showed that peaks in density at this station occurred unpredictably, and there was no evidence of any seasonal variation.

The reasons for these obvious differences in annual variations in population density which existed between the upstream area and the downstream area relate to fundamental differences between the two habitats, which are discussed in detail in Section C.

## B(iv) Population Size Structure

### Introduction

Population size structure has been determined in previous studies on freshwater triclads (e.g. Reynoldson 1961a) to establish the timing, duration and extent of specific demographic events (e.g. population recruitment). Such information is obtained by collecting data regularly on the relative abundance of different size classes (in triclads, size classes are normally considered in terms of body length) within particular populations. Unfortunately, these size classes cannot be correlated with age, due to the fact that triclads are able to degrow (or shrink) in response to situations of poor resource availability (Calow and Woollhead 1977). Thus it is not possible to assess the age structure of a triclad population using similar methods as have been employed for other animals e.g. lotic insect populations (Elliot 1982). Despite this, information on population size structure is useful in establishing the occurrence of reproductive events, and together with direct information on reproduction (see next section) helps to provide a comprehensive assessment of the reproductive processes of the population considered here.

Specifically, the aims of this section are as follows: (i) To consider the existence of within- and between-station differences in population size structure over the sampling period. (ii) To relate these, where they exist, to specific demographic events occurring within the population.

In previous studies on exclusively sexual species of freshwater triclads, the interpretation of changes in size-structure within populations has proved relatively straightforward. All recruitment derives from eggs (excluding immigration), and the hatching and subsequent maturation of individuals from these can be observed in size/frequency histograms as a predictable, pulsed event (Reynoldson 1961a).

When sexual and asexual reproduction occurs within the same population, as in the population of <u>C.alpina</u> considered here, recruitment is derived from both sexually produced eggs and asexually produced fission products. Although in such a population, pulsed events relating to the growth to 'maturity' of a cohort of individuals may be distinguishable in terms of changes in population size structure through time, data on size structure alone are insufficient to establish whether such pulsed events are sexual or asexual in nature. In order to assess the relative contributions of sexual and asexual reproduction to population growth, it is necessary to know the relative numbers of sexual and asexual individuals in the population throughout the study period, and this will be discussed in the following section.

To comment fully on the results presented in this section, therefore, it is also necessary to consider the results presented in the following section on reproductive profile. This section is therfore concerned primarily with identifying variation in population size structure between and within stations; where possible, specific explanations for these differences will be given in the discussion section at the end of this chapter.

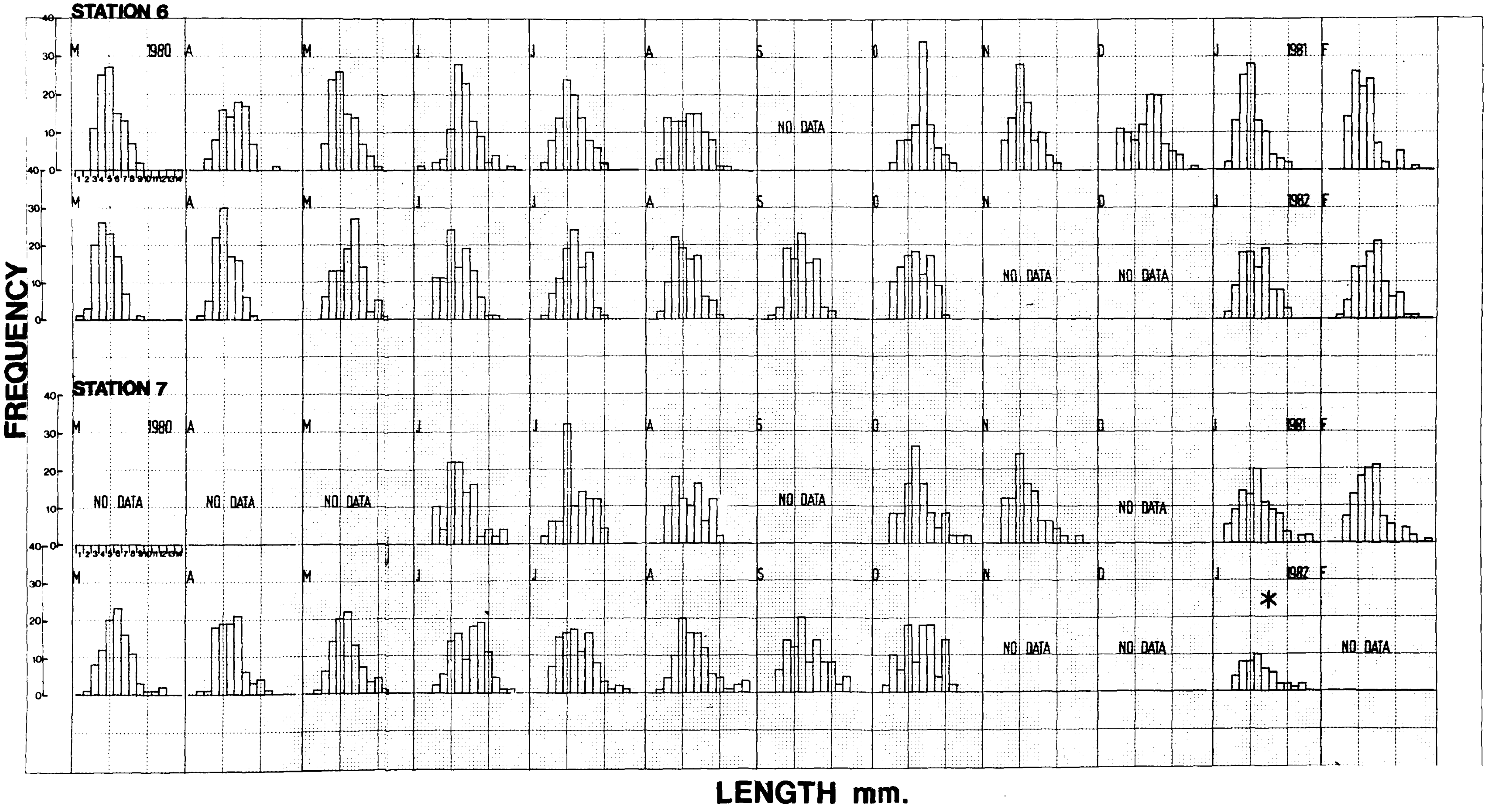
## Methods

Individuals were collected at each station on a monthly basis over the period March 1980 to February 1982. Animals were obtained by picking up stones from the bed of the stream at random, picking off triclads with a fine paintbrush and placing them in a perspex container filled with fresh stream water. This process was repeated until 100 animals had been collected. Subsequently, the samples from each station were placed in a thermally insulated 'Camping Gaz' coolbox to prevent overheating on the journey back to the laboratory.

Immediately on return to the laboratory, the animals were assessed for size and reproductive type. Size was measured as follows: Animals from each station were decanted into a large crystallising dish, which was placed over a laminated sheet of graph paper (1mm Chartwell). Size was estimated by measuring the length of each individual triclad as it glided over the graph paper background. The distance between the top of the head and the tip of the tail was chosen as an index of size since the other two indices - area and weight - were unsuitable: area because it was an expensive technique, involving the photographing of individual animals (Woollhead 1979), and weight, because animals tended not to survive the measuring process (Woollhead ibid).

Assessment of reproductive type was carried out concurrently with the size measurements. The method of classification into the three categories: 'Sexual', 'asexual' and 'immature' is described in detail in the following section. For the purposes of this section, only these three general categories are considered.

Having completed the analysis, the samples were placed in cooled incubators (October to March caught animals : 5C; April to September caught animals : 10C) until their return to the sampling area, when the animal samples were returned to their respective points of collection.


STATION 6
M 1980
A
M
J
J
A
S NO DATA
O
N
D
J 1981 F
M
A
M
J
J
A
S
O
N NO DATA
D NO DATA
J 1982 F
STATION 7
M 1980 NO DATA
A NO DATA
M NO DATA
J
J
A
S NO DATA
O
N
D NO DATA
J 1981 F
M
A
M
J
J
A
S
O
N NO DATA
D NO DATA
J 1982 F NO DATA
*
0
10
20
30
40
1 2 3 4 5 6 7 8 9 10 11 12 13 14
FREQUENCY
LENGTH mm.

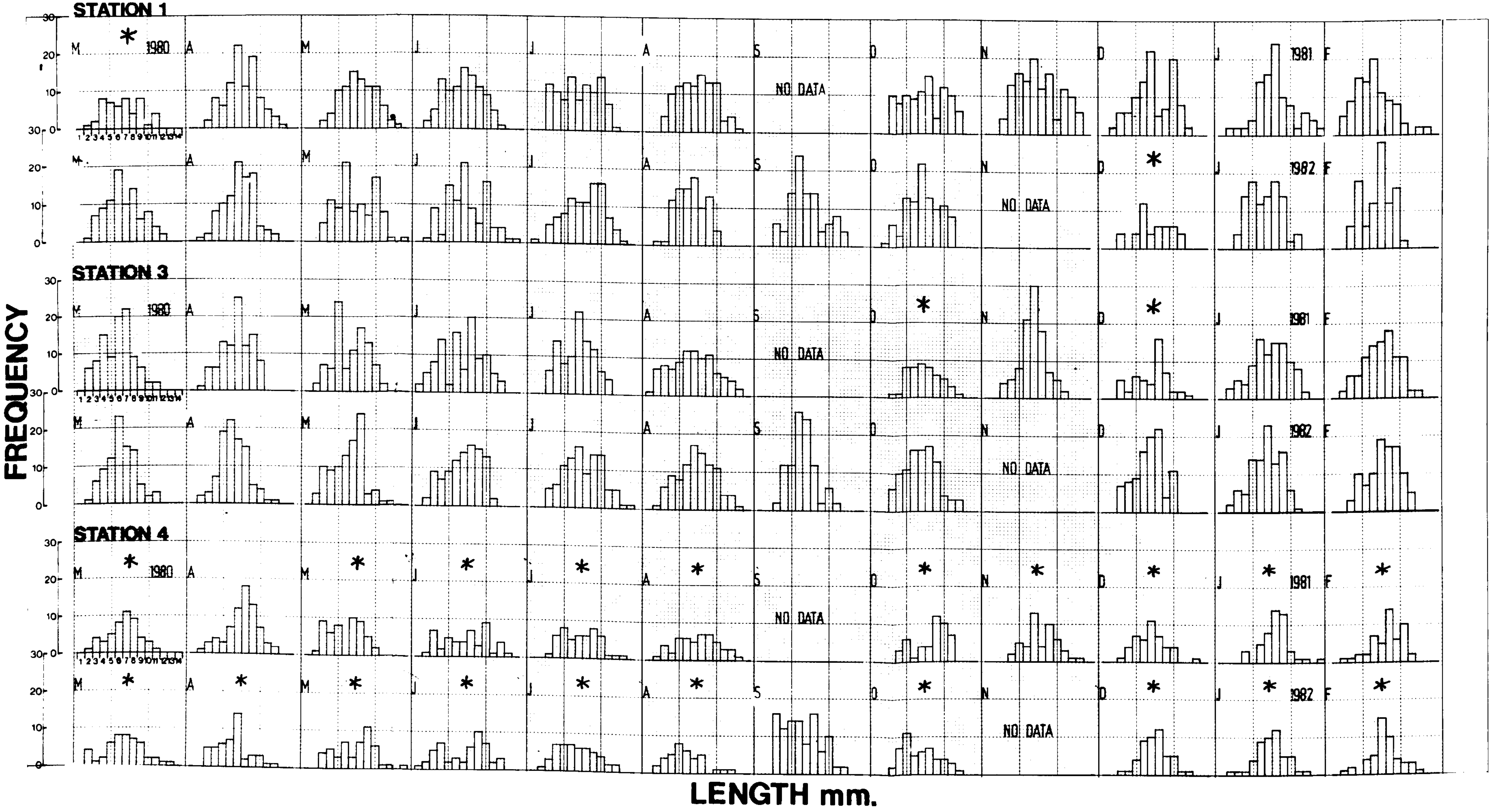

STATION 1
STATION 3
STATION 4
M A M J J A S O N D J F
1980
1981
1982
NO DATA
*
0
10
20
30
1 2 3 4 5 6 7 8 9 10 11 12 13 14
FREQUENCY
LENGTH mm.

FIGURE 26

monthly size-frequency distributions of C.alpina from stations 1,3,4,6 and 7 over the period March 1980 to February 1982

n = 100 for all samples, except (*) - n = 50

The range in individual triclad size was similar for all sites studies: 1-14 mm in length (N.B. station 6: 1-13 mm). This range is broadly similar to that described for other British populations of this species by Burkill (1957), Wright (1968) and Lock (1972a).

Size-frequency histograms showing the change in size structure of the population at the five sampling stations chosen over the period March 1980 to February 1982 are given in Figure 26. For reasons mentioned above, accurate interpretation of these data was complicated because sexual and asexual reproduction occurred at all stations. However, there seemed little evidence at any station for any pronounced period of recruitment (considered as an increase in the number of animals in the juvenile size classes - defined here as animals less than 5mm in length, 6mm being the critical size at which sexual maturity can be distinguished) over the sampling period. This can be seen clearly in Figure 27, where the number of juveniles in each sample is given as a percentage, and summarised for each station over the period March 1980 to February 1982. Although significant 'peaks' occurred, these tended to appear unpredictably, and the overall trend at all five stations was one of constancy.

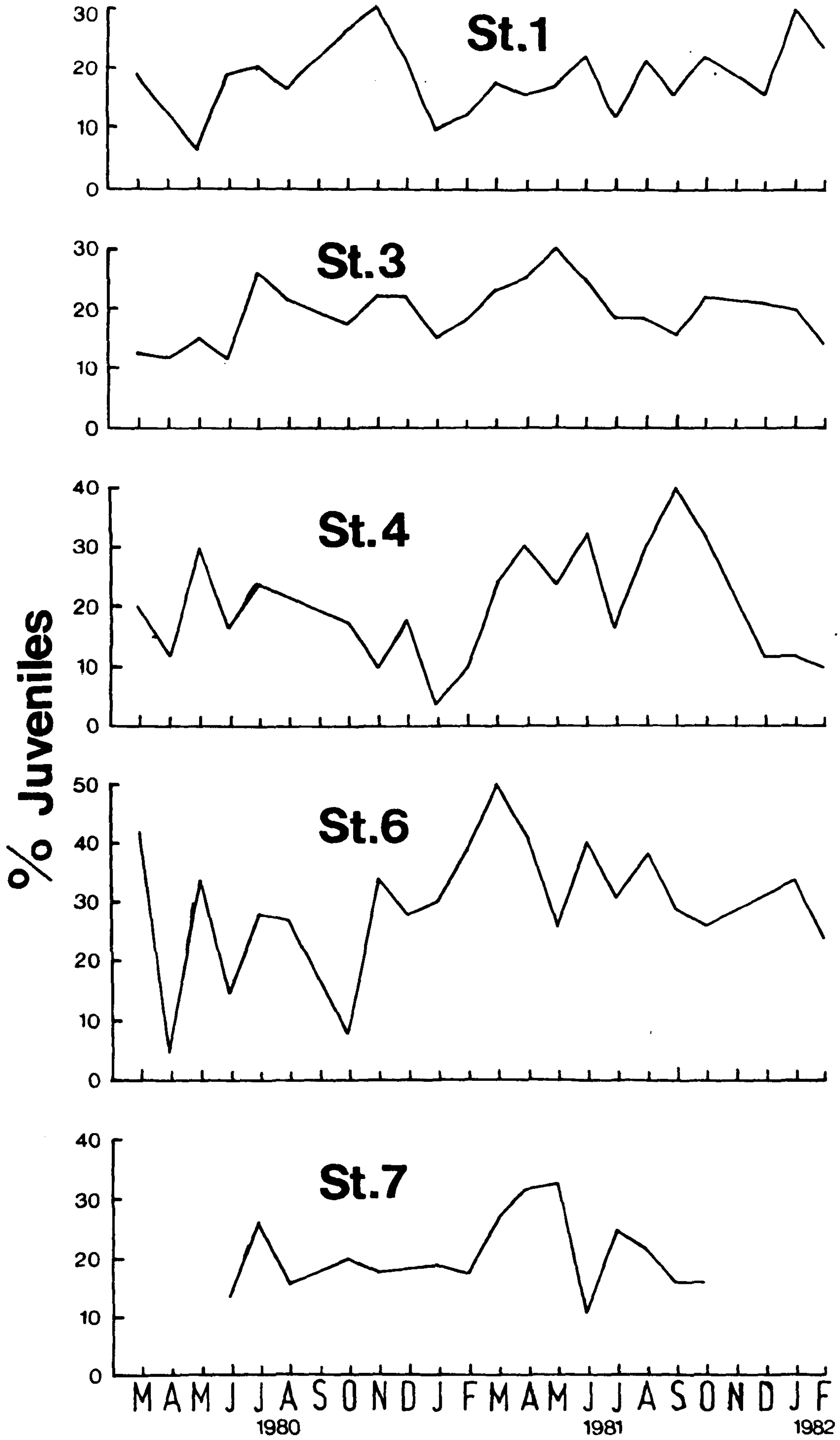
There are two possible explanations for this lack of any detectable 'breeding season':

(i) No such period occurred at any of the stations during the sampling period.

(ii) Significant 'peaks' in sexually derived recruitment were masked by concurrent 'troughs' in asexually derived

# FIGURE 27

% Juveniles (i.e. animals <5mm) in monthly samples for stations 1,3,4,6 and 7 over the period March 1980 to February 1982


% Juveniles
St.1
30
20
10
0
St.3
30
20
10
0
St.4
40
30
20
10
0
St.6
50
40
30
20
10
0
St.7
40
30
20
10
0
M A M J J A S O N D J F M A M J J A S O N D J F
1980
1981
1982

SAMPLING STATIONS

| | 1 | | 3 | | 4 | | 6 | | 7 | |
|---|---|---|---|---|---|---|---|---|---|---|
| | $\bar{x}$ | S.D. | $\bar{x}$ | S.D. | $\bar{x}$ | S.D. | $\bar{x}$ | S.D. | $\bar{x}$ | S.D. |
| 1980 | | | | | | | | | | |
| MAR | 6.63 | (2.35) | 5.89 | (2.09) | 6.63 | (2.07) | 5.23 | (1.51) | ** | ** |
| APR | 7.52 | (2.35) | 6.81 | (2.03) | 7.62 | (2.15) | 5.82 | (2.51) | ** | ** |
| MAY | 7.69 | (2.13) | 6.60 | (2.23) | 6.00 | (2.27) | 5.48 | (1.62) | ** | ** |
| JUN | 6.88 | (2.37) | 6.72 | (2.78) | 7.35 | (3.00) | 6.79 | (1.97) | 6.42 | (2.17) |
| JUL | 6.85 | (2.76) | 6.79 | (2.15) | 7.24 | (2.39) | 5.71 | (1.78) | 6.20 | (1.97) |
| AUG | 7.31 | (2.40) | 6.84 | (2.87) | 7.48 | (2.73) | 5.69 | (2.06) | 6.28 | (2.49) |
| SEP | ** | ** | ** | ** | ** | ** | ** | ** | ** | ** |
| OCT | 7.39 | (2.74) | 7.42 | (2.05) | 8.36 | (2.18) | 6.12 | (2.62) | 6.56 | (2.38) |
| NOV | 6.67 | (1.93) | 6.86 | (1.69) | 7.92 | (2.08) | 5.98 | (1.98) | 6.00 | (2.25) |
| DEC | 7.32 | (2.52) | 7.12 | (2.23) | 6.93 | (2.42) | 6.55 | (2.42) | ** | ** |
| 1981 | | | | | | | | | | |
| JAN | 8.02 | (2.49) | 7.36 | (2.42) | 8.04 | (1.84) | 5.10 | (1.69) | 6.00 | (2.43) |
| FEB | 6.00 | (2.43) | 7.03 | (2.27) | 7.76 | (2.05) | 5.19 | (1.78) | 6.26 | (2.17) |
| MAR | 6.73 | (2.35) | 6.32 | (1.93) | 6.88 | (2.56) | 4.55 | (1.40) | 5.96 | (1.91) |
| APR | 7.18 | (2.03) | 6.47 | (1.78) | 6.27 | (2.36) | 5.38 | (1.41) | 6.01 | (1.73) |
| MAY | 7.28 | (2.53) | 6.33 | (2.16) | 7.39 | (2.56) | 6.29 | (1.79) | 5.79 | (1.92) |
| JUN | 7.28 | (2.62) | 6.96 | (2.32) | 7.12 | (3.05) | 5.93 | (1.83) | 7.49 | (2.12) |
| JUL | 7.71 | (2.56) | 6.07 | (2.66) | 6.74 | (2.52) | 5.97 | (1.67) | 6.37 | (2.20) |
| AUG | 6.98 | (2.14) | 7.30 | (2.46) | 6.68 | (2.74) | 5.46 | (1.76) | 6.56 | (2.32) |
| SEP | 7.04 | (2.32) | 6.47 | (1.74) | 10.12 | (2.90) | 5.97 | (1.68) | 6.71 | (2.36) |
| OCT | 7.22 | (2.23) | 6.90 | (2.20) | 6.76 | (2.37) | 6.02 | (1.87) | 6.64 | (2.30) |
| NOV | ** | ** | ** | ** | ** | ** | ** | ** | ** | ** |
| DEC | 7.35 | (2.30) | 6.76 | (1.96) | 7.28 | (1.97) | ** | ** | ** | ** |
| 1982 | | | | | | | | | | |
| JAN | 6.62 | (2.06) | 6.76 | (2.02) | 7.34 | (1.95) | 5.82 | (1.94) | 6.23 | (2.29) |
| FEB | 6.48 | (1.92) | 7.28 | (2.19) | 7.38 | (2.05) | 6.31 | (2.13) | ** | ** |
| $\bar{X}$ | 7.14 | | 6.82 | | 7.13 | | 5.84 | | 6.23 | |

N.B. ** = missing data

Table 25 : Triclad size (mm.) - monthly means and standard deviations calculated from the data presented in Figure 26 for stations 1,3 4,6 and 7 over the period March 1980 to February 1982 - see text.

## FIGURE 28

Size-frequency histograms obtained by pooling data at stations 1,3,4,6 and 7 over the period March 1980 to February 1982

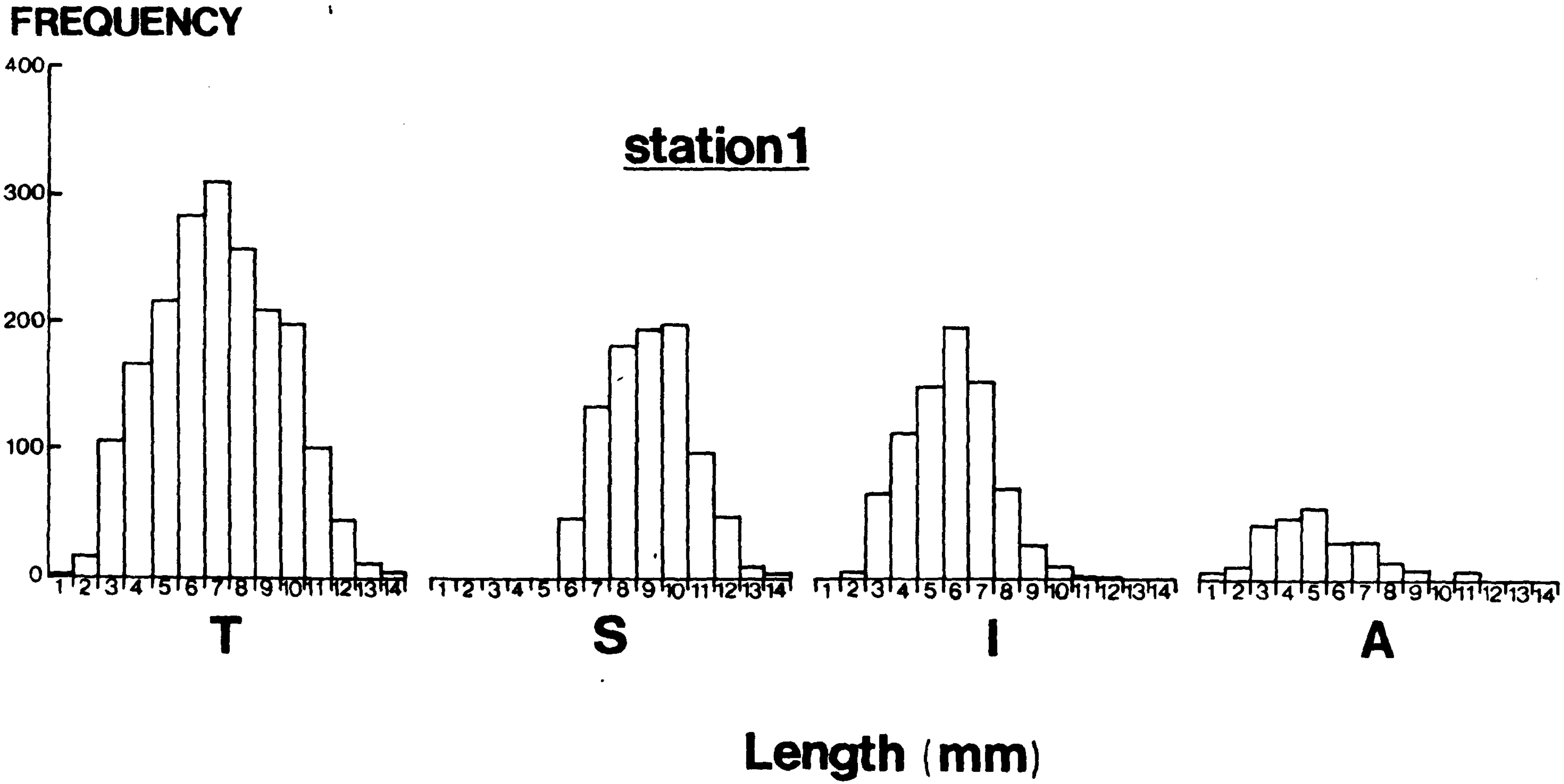
T = total size-frequency distribution
(represents all animals collected)

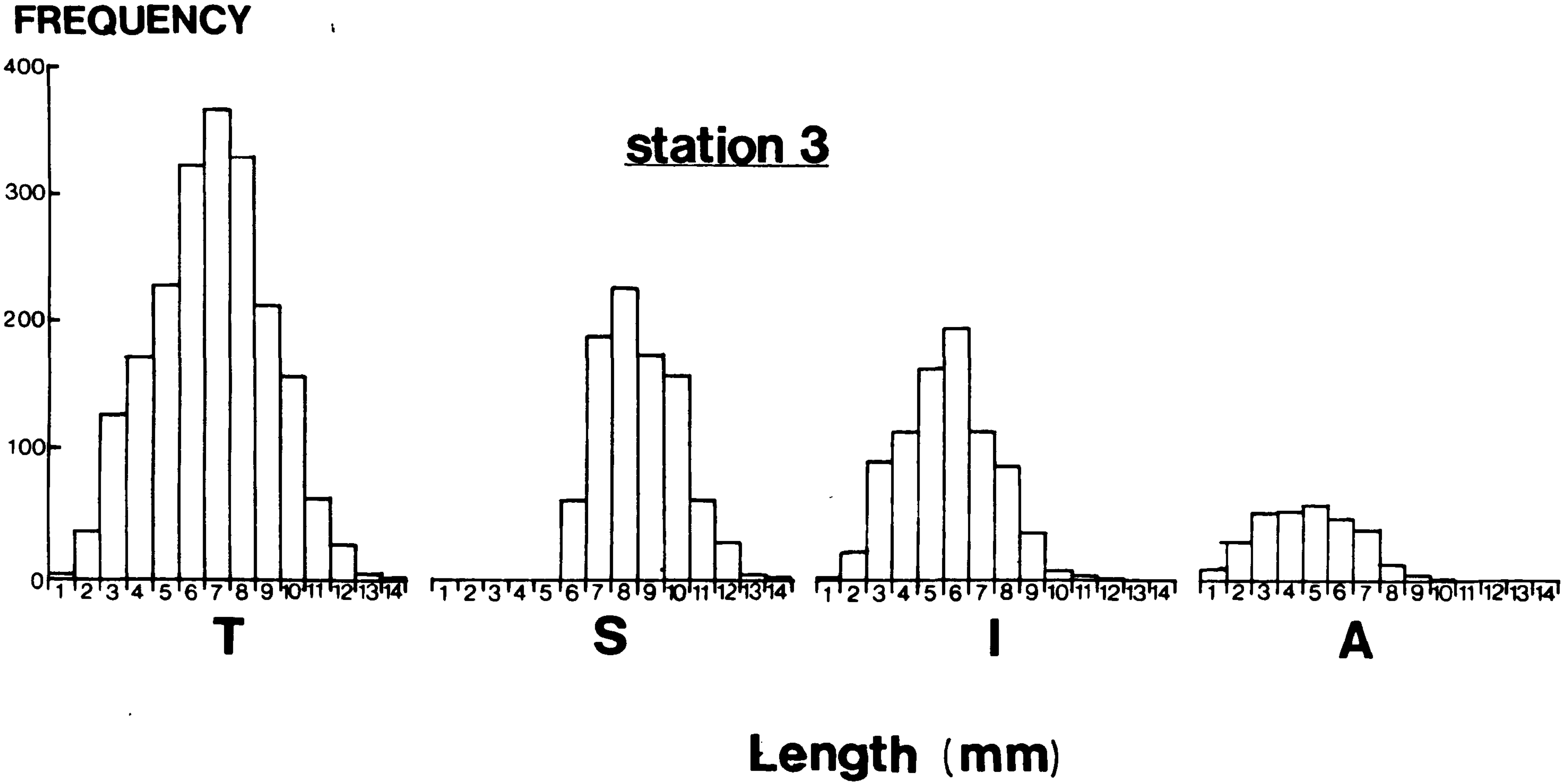
S = 'sexual' size-frequency distribution
(represents all sexual animals)

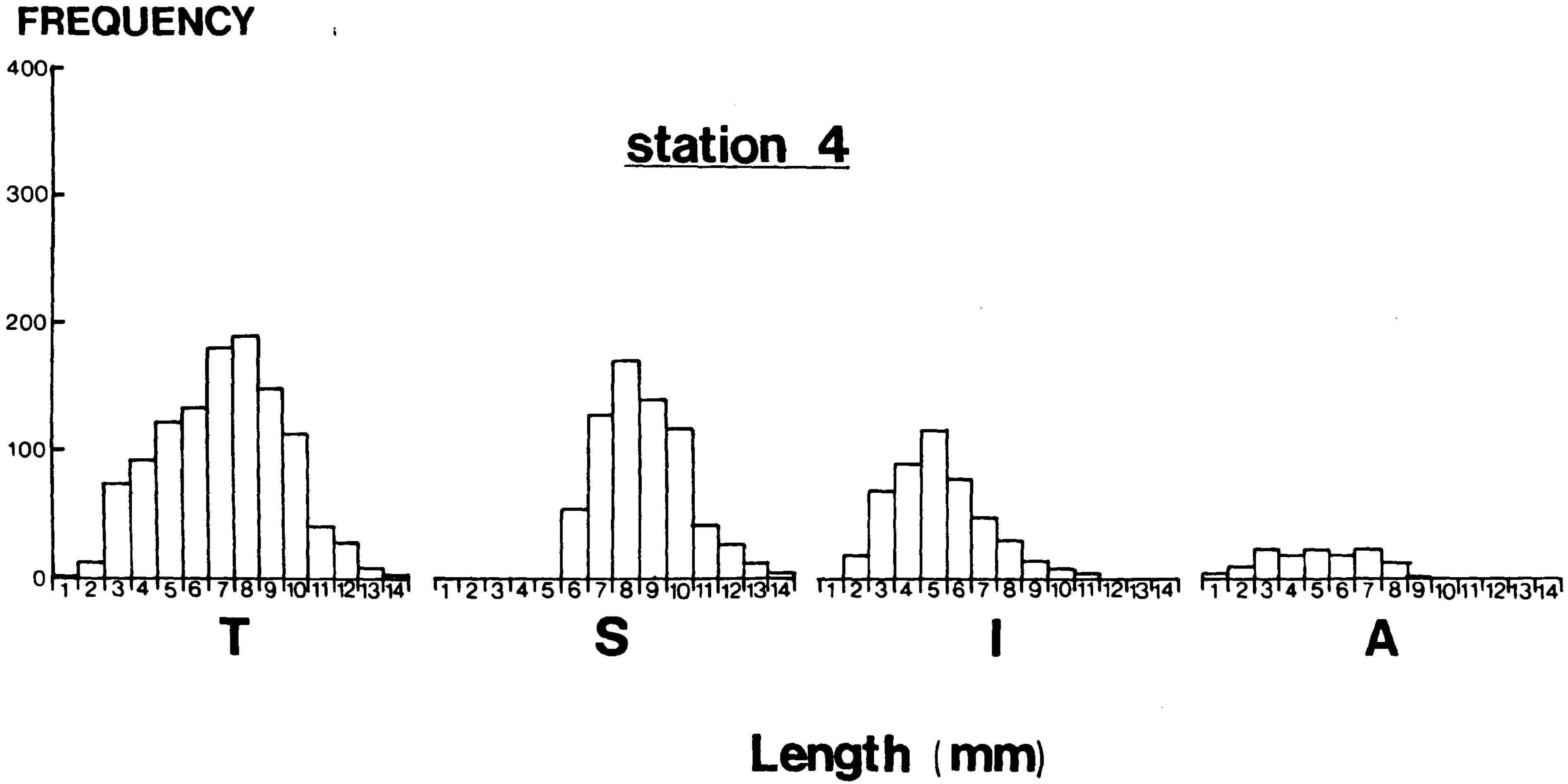
I = 'immature' size-frequency distribution
(represents all immature animals)

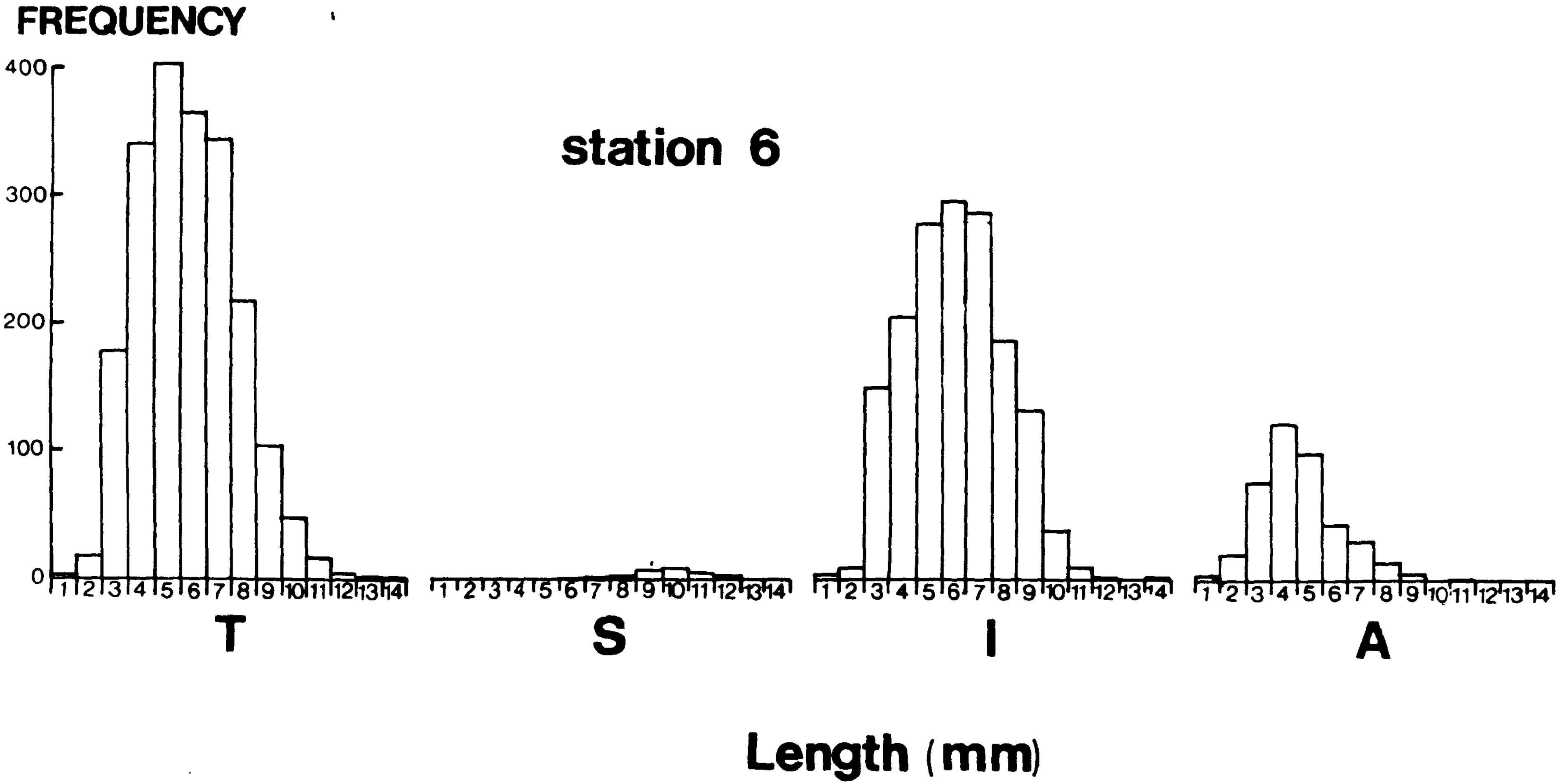
A = 'asexual' size-frequency distribution
(represents all asexual animals)

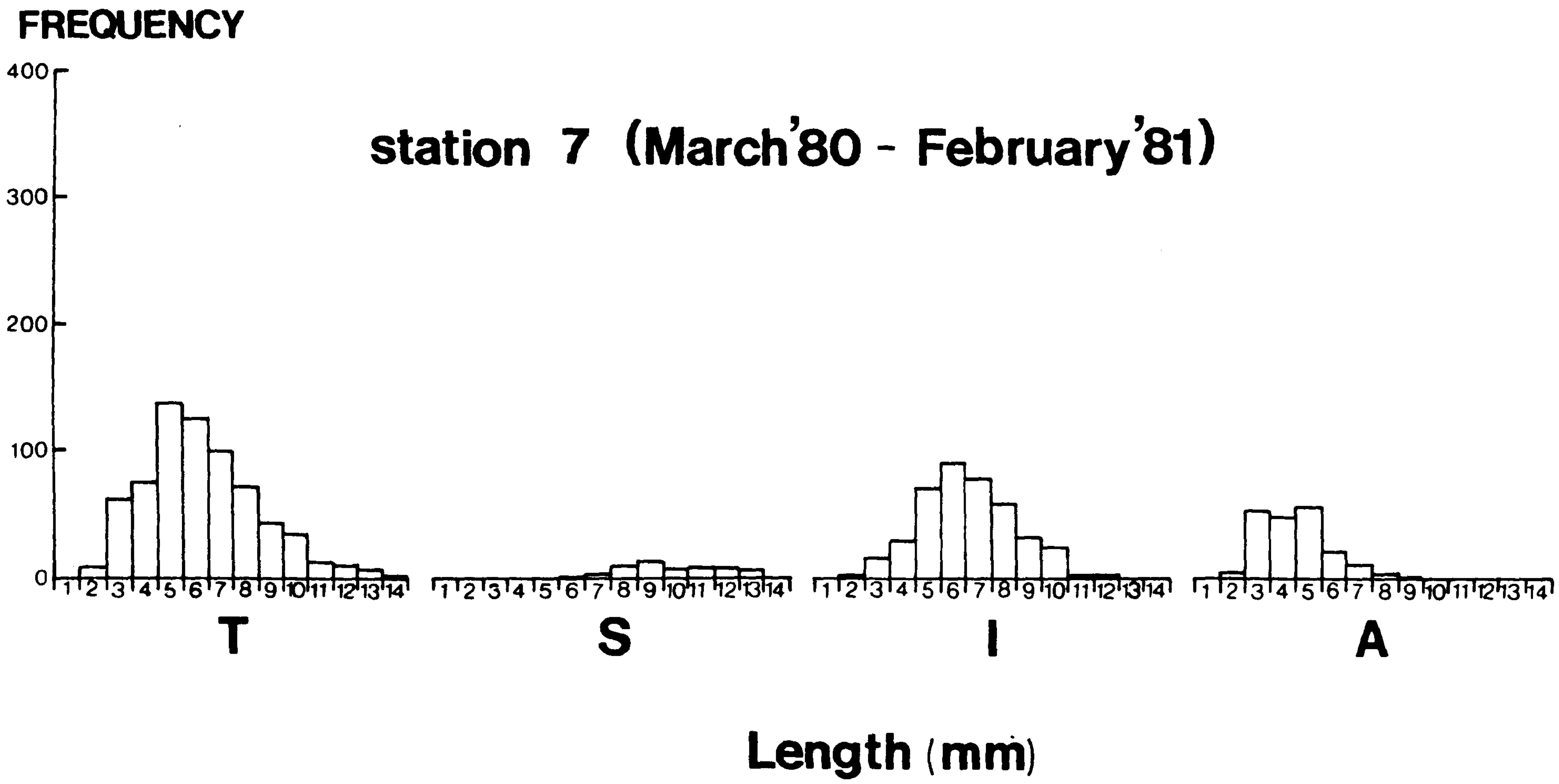
N.B. Data for station 7 was pooled separately for the periods June 1980 to February 1981, and March 1981 to February 1982, for reasons described in the text.

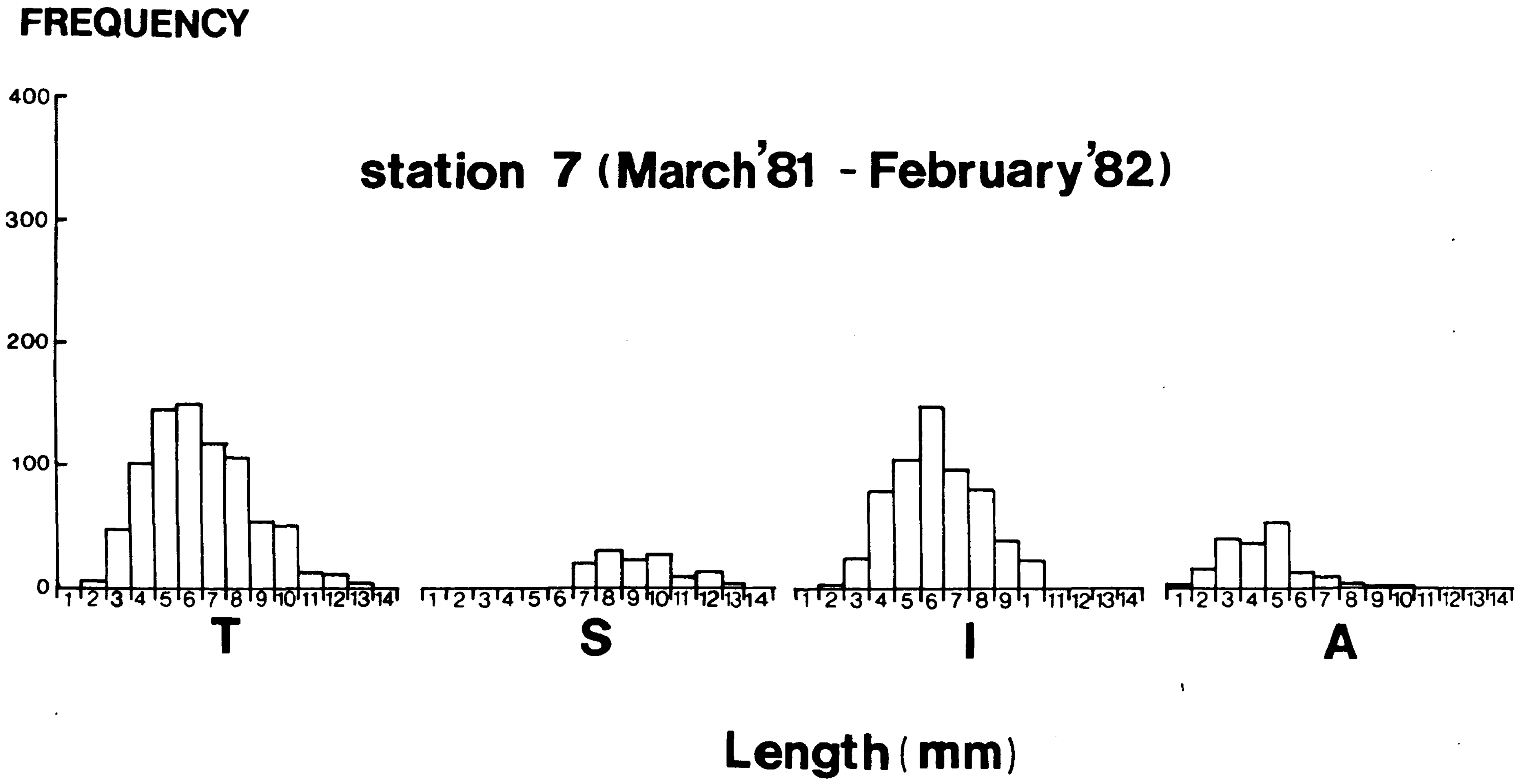

FREQUENCY
400
300
200
100
0
station1
1 2 3 4 5 6 7 8 9 10 11 12 13 14
T
1 2 3 4 5 6 7 8 9 10 11 12 13 14
S
1 2 3 4 5 6 7 8 9 10 11 12 13 14
I
1 2 3 4 5 6 7 8 9 10 11 12 13 14
A
Length (mm)


FREQUENCY
400
300
200
100
0
station 3
1 2 3 4 5 6 7 8 9 10 11 12 13 14
T
1 2 3 4 5 6 7 8 9 10 11 12 13 14
S
1 2 3 4 5 6 7 8 9 10 11 12 13 14
I
1 2 3 4 5 6 7 8 9 10 11 12 13 14
A
Length (mm)


FREQUENCY
400
300
200
100
0
station 4
1 2 3 4 5 6 7 8 9 10 11 12 13 14
T
1 2 3 4 5 6 7 8 9 10 11 12 13 14
S
1 2 3 4 5 6 7 8 9 10 11 12 13 14
I
1 2 3 4 5 6 7 8 9 10 11 12 13 14
A
Length (mm)

FREQUENCY
400
300
200
100
0
station 6
1 2 3 4 5 6 7 8 9 10 11 12 13 14
T
1 2 3 4 5 6 7 8 9 10 11 12 13 14
S
1 2 3 4 5 6 7 8 9 10 11 12 13 14
I
1 2 3 4 5 6 7 8 9 10 11 12 13 14
A
Length (mm)


FREQUENCY
400
300
200
100
0
station 7 (March'80 - February'81)
1 2 3 4 5 6 7 8 9 10 11 12 13 14
T
S
I
A
Length (mm)


FREQUENCY
400
300
200
100
0
station 7 (March'81 - February'82)
1 2 3 4 5 6 7 8 9 10 11 12 13 14
1 2 3 4 5 6 7 8 9 10 11 12 13 14
1 2 3 4 5 6 7 8 9 1 11 12 13 14
1 2 3 4 5 6 7 8 9 10 11 12 13 14
T
S
I
A
Length (mm)

recruitment and vice versa.
Clearly, choosing between these two explanations requires more precise information and no further comment is made on this until the next section.

Differences between stations in overall population size structure conform to a pattern similar to that already outlined for the density estimates given in the previous section.

The data presented in Table 25 give the mean size and standard deviation for each of the monthly samples collected for each station. It can be seen that the samples collected from the downstream stations (1, 3 and 4) always exhibit mean values which are higher than corresponding values from the upstream stations (6 and 7). It should again be emphasised that any comparison between stations excludes data from station 7 collected after March 1981 (for reasons given in the previous section). Although an analysis of variance was initially considered as a means of testing the statistical significance of these differences, non-normal distributions in some of the data suggested that this method would not be generally applicable. This is illustrated when the data presented in Figure 26 are pooled to construct overall size-frequency histograms for each station, as in Figure 28. In stations 1 and 3, the total pooled size-frequency data apparently conform to a normal distribution; whereas in stations 6 and 7 (data for station 7 from the period March 1980 to February 1981), and also possibly in station 4, the pooled total size-frequency data appear highly

| 3 | 4 | 6 | 7 | |
|---|---|---|---|---|
| 0.07* | 0.03 | 0.24* | 0.19* | 1 |
| | 0.07 | 0.21* | 0.17* | 3 |
| | | 0.27* | 0.22* | 4 |
| | | | 0.08 | 6 |

* = denotes sig. at p=0.05

TABLE 26 : Values of Dmax calculated using the Kolmogorov-Smirnov two tailed test for large samples, comparing the total size-frequency distributions for stations 1,3,4,6,and 7 shown in Fig. 28

skewed. In order to test for significant differences in the patterns of the total size-frequency distributions between stations, the distributions were compared using the two-tailed version of the Kolmogorov-Smirnov Test (Siegel 1956). The results of this test are given in Table 26, in which values of Dmax indicate the degree of difference between the distributions at each station (Dmax increases proportionally with the degree of difference between the two distributions compared). As expected, the highest Dmax values occurred in comparisons between upstream and downstream stations.

The reasons for the difference in the shape of the distributions between stations relates to the fact that although both sexual and asexual reproduction occurred throughout the study area, the relative importance of these two forms of reproduction varied among the stations sampled.

When the pooled data for each station are broken down into reproductive categories ('sexual', 'asexual' and 'immature' - an explanation of this method of classification is given in the next section), and the three resulting size-frequency distributions are contructed for each station (also given in Figure 28), the reasons for the differences in shape of the total size-frequency distributions for each station become apparent. The 'normal' distribution curves exhibited by stations 1 and 3 are the result of the addition of two oppositely skewed curves (corresponding to the size distributions of 'sexual' and 'asexual' animals) to a 'normally' distributed curve (corresponding to the size distribution of 'immature' animals). In contrast, the skewed distribution curves exhibited by stations 6 and 7 are the result of the addition of one skewed curve (the 'asexual' animals) to a normally distributed curve (the 'immature' animals); in these cases the relatively small number of sexual animals has failed to 'balance' the larger number of asexual animals, causing the total size distribution curves at both stations to become skewed towards the smaller size range.

It seems, therefore, that the shapes of the total size distributions presented in Figure 28 are indicative of the relative intensity of sexual and asexual reproduction exhibited by the population of _C.alpina_ at each station. This is due to the fact that, in general, sexual animals were larger than asexual animals. The occurrence of greater numbers of larger, sexual animals in the downstream area relative to the upstream area explains the differences in mean size between the two areas apparent from Table 25.

## B(v) Reproduction

### (a) Introduction

This section gives a detailed account of the reproductive processes exhibited by _C.alpina_ in the population studied, and reviews the relevant literature concerning various aspects of reproduction in this species (which was omitted from Chapter 2). Due to the complex nature of the reproductive processes exhibited by

C.alpina, sexual and asexual reproduction (my definitions - see Chapter 1) are initially treated separately, although a linking discussion is included following the presentation of results on both aspects.

## (b) Sexual Reproduction

In common with the majority of turbellarian species, C.alpina is a simultaneous hermaphrodite. The organisation of its reproductive system is described in detail by Ball and Reynoldson (1982), and consists of two anteriorly positioned ovaries which are linked to the copulatory bursa by separate ovovitelline ducts. The yolk glands which open into these ducts are scattered throughout the body, but unlike many other species, the testes are only distributed posteriorly as far as the anterior tip of the pharyngeal region. The copulatory complex is a distinctive feature in this species, particularly characteristic are the thick muscle plates of the genital atrium. The penis is composed of a small bulb and a long papilla which extends into the atrium; the vasa deferentia link the penis with the testes, but do not form an enlarged seminal vesicle. The copulatory complex can be recognised as an unpigmented hump situated posteriorly to the pharyngeal region on the dorsal surface of intact animals, and becomes particularly conspicuous during the later stages of maturation (see Fig 29 ).

In copulation, sperm is transferred between individuals and stored initially in the copulatory bursa, before being transferred to a receptaculum seminis, situated behind each ovary (Ball and Reynoldson ibid). Eggs are fertilised as they pass down the ovovitelline ducts, and are finally stored, together with yolk material from the yolk glands, in a preformed cocoon situated in the genital atrium. Following deposition, the cocoon turns from its initially pale brown colour to a dark brown, due to a tanning process. In _C.alpina_, cocoons are laid unattached to the substratum, although they are normally deposited in crevices, presumably to avoid dislodgement in lotic conditions.

Being a hermaphrodite, it is theoretically possible for _C.alpina_ to produce self-fertilised eggs; although there is no recorded instance of this occurring, such a phenomenon has been reported for other related species (Biersma and Wisjman 1981). In the population studied, copulating animals were found on numerous occasions throughout the study period.

Cocoon production in the majority of triclads occurs seasonally. In the British Isles, most lake-dwelling species produce cocoons in spring and early summer, although the exact timing varies between species (Ball and Reynoldson 1982). In contrast, the stream-dwelling species, and in particular _C.alpina_, produce cocoons in winter (Carpenter 1928; Beauchamp 1933), supposedly being limited to asexual reproduction for the remainder of the year (see below). In general, the seasonal production of cocoons by British species seems to be controlled by water temperature, with the upper temperature limit preventing breeding in most species, e.g. _Dugesia polychroa_

(O.Schmidt) is more tolerant of high temperature conditions than Dendrocoelum lacteum (O.F.Muller), the former being able to produce cocoons up to temperatures of 23C, whereas the latter is constrained due to the fact that its reproductive system fails to develop at temperatures in excess of 18.5C (Sefton and Reynoldson 1972). As mentioned in Chapter 2, there is a great deal of controversy concerning the influence of water temperature on the distribution of C.alpina in freshwater habitats in Europe. This controversy extends similarly to the influence of water temperature on sexual reproduction.

Steinmann (1907) was the first to propose that the ability of C.alpina to reproduce sexually was limited by high temperatures, quoting an upper limit of 5-6C. This 'upper limit' was modified by a number of authors: e.g. Thienemann (1912) 3-12C, Carpenter (1928) 7-10C. Beauchamp (1933) carried out laboratory experiments, which indicated a maximum temperature for sexual reproduction of 10C. From these experiments, together with observations carried out on a population inhabiting a stream near Lake Windermere, he developed a rudimentary model to explain the changes he found occurring in the population at different times of year. Described simply, this model suggests that an annual cycle of reproduction occurs in this species which is linked to large scale population movements: In late autumn, a fall in water temperature coupled with an increase in nutritional state (following storage of surplus resources accumulated over the summer) causes a behavioural change such that triclads migrate upstream en masse, maturing sexually as they do so. Upon reaching the headwaters of the stream, the animals breed, deposit cocoons and thus gradually reduce their internal food reserves. At the onset of spring, another behavioural change occurs, due to the increasing temperature of the habitat and the subsequent 'de-maturation' process following reproduction and depletion of food reserves. The result of this second behavioural change is another mass migration downstream into warmer water in order to feed, re-attain sexual maturity and hence repeat the whole process the following autumn. Apart from direct field observation, Beauchamp (1932, 1933, 1935) claimed laboratory evidence to support this hypothesis. He stated that he could induce persistent positive rheotaxy (movement against a current) by feeding individuals until they became sexually mature, and that persistent negative rheotaxy (downstream movement) could be induced in positively rheotactic individuals by starving them (thus depleting their food resources and causing gonad resorption). He produced further evidence to support his claims by reporting that all animals obtained from the field with recently matured, ripe gonads were always consistently positively rheotactic, and all animals with 'spent' gonads (following cocoon deposition) showed negative rheotaxis. That this rather dubious hypothesis has remained in the literature up to the present day as a 'classic' example of invertebrate migration (e.g. Baker 1978) is surprising, when it is considered that both the phenomenon of upstream/downstream migration and the relationship between state of gonad maturation and response to current flow were convincingly disproved by Burkill (1957). She showed that both in a population of C.alpina near Cambridge and in Beauchamp's original Windermere population, there was no evidence of any migration at any time of the year, and no aggregation of sexually mature animals at the headwaters in winter. In the laboratory, although she confirmed some of Beauchamp's (1932) observations on the influence of feeding on rheotaxy, she found no evidence to support a link between rheotaxy and gonad condition. Also, all individuals were found to exhibit spontaneous changes in rheotactic behaviour in the absence of any external stimuli. Admittedly, Beauchamp (1937) altered his model in the light of later laboratory results, but this modification still presupposed a behavioural difference relating to gonad maturity, and furthermore, as Burkill (1957) pointed out, was "untestable".

It was Dahm (1958) who was the first to carry out rigorous experiments on reproduction in this species. He recognised three distinct types of population, separable on the criterion of mode of reproduction: Strictly asexual populations, strictly sexual populations, and populations exhibiting both sexual and asexual reproduction. In purely sexual populations, he found that in the laboratory, cocoon production occurred over the temperature range 6-12C, and that the level of production increased with increasing ration level. Similarly in populations showing sexual and asexual reproduction, cocoon production was limited by temperatures above 10C, and was again enhanced by increased ration level. (Relevant information from this study concerning asexual reproduction is considered later in this section.)

Wright (1968) provides similar evidence in his study on Welsh populations of *C.alpina*, in which he fed (for 10 weeks) and subsequently starved (for 6 months) animals from various locations in order to assess their reproductive capabilities (the rationale arising from Dahm (1958)). He found populations apparently conforming to Dahm's three types (i.e. sexual, sexual and asexual and asexual), and noted that the strictly sexual populations occurred only in high altitude spring habitats (i.e. in stenothermal conditions – see Chapter 2), but that in these populations sexual reproduction occurred throughout the year. This statement was based on the fact that copulating animals occurred throughout the year, and animals caught in winter and summer both produced cocoons on return to the laboratory. He concluded that sexual reproduction was 'not limited to winter' in these populations, but also noted that the habitats in which they occurred effectively provided a 'winter' thermal regime throughout the year.

To conclude this short review, it can be said that in an examination of the literature relating to the influence of temperature on sexual reproduction in *C.alpina*, similar conclusions can be drawn as were described in Chapter 2 for the influence of temperature on distribution, i.e. that *C.alpina* exists throughout its range as a series of locally adapted populations, whose physiological responses to temperature (in terms of reproduction, survivorship, oxygen consumption etc.) are directly linked to the prevailing conditions in the habitat in which they live. In otherwords, animals inhabiting stenothermal situations would be expected to show stenothermic physiological responses under laboratory conditions. It is therefore misleading to use results obtained from individual populations as measures of the ecological plasticity of the species as a whole. This argument, which I believe to be central to the understanding of the ecology of this species, will be restated in the final section of this chapter, together with supportative evidence gained during the course of this study.

In previous studies, other factors have been noted which influence sexual reproduction in C.alpina: ration level has already been mentioned, and the evidence to support this seems unequivocal (Dahm 1958). Reynoldson and co-workers (for references see Ball and Reynoldson 1982) and Calow and Woollhead (1977) have shown that the ability of lake-dwelling triclad species to obtain and partition resources effectively, particularly under situations of low resource availability, is of equal, if not greater importance than temperature as a constraint on reproductive output.

There is much evidence to suggest that populations of C.alpina are resource limited either by interspecific competition (e.g. with P.felina (Beauchamp and Ullyott 1932)) or by intraspecific competition (Lock and Reynoldson 1972) in some situations, yet both possibilities remain largely unproven (for a brief discussion of the evidence, see Chapter 2). However, the fact that populations of C.alpina are known to exist at high densities in many locations (Wright 1968), and considering the generally poor trophic quality of stream habitats in the British Isles (Reynoldson 1953: it should be noted, however, that this assumption, though probably correct, is based on rather scanty evidence), it seems likely that intraspecific competition is playing a limiting role in these populations. Similarly the effects of intraspecific competition on the occurrence of sexual reproduction in such populations can only be speculated upon, but they are likely to be significant (see concluding discussion).

Dahm (1958) also noted that cytogenetic factors seemed to be of some importance in influencing sexual development. When he examined the interrelationship between polyploidy and reproduction in this species, he noticed that individuals with certain karyotypes exhibited irregular forms of gametogenesis, resulting in the production of infertile cocoons. He failed, however, to find any concrete evidence to link karyotype with the ability to exhibit sexual characteristics.

Although recent reviews would suggest otherwise (e.g. Ball and Reynoldson 1981), it is apparent that despite considerable research, the anatomical mechanisms involved in sexual reproduction in this species are more clearly understood than the ecological mechanisms.

The results presented below, concerning the occurrence of sexual reproduction in the study area are discussed in Section C in relation to other work carried out in previous studies (described above). In Section C, the ecological mechanisms which are influencing sex within the study populations of C.alpina are considered, together with the wider implications of the results for the species as a whole.

## Methods

The evidence presented in this section seeks to establish the level and duration of sexual reproduction in the study population at each of the sampling stations chosen over a two year period. It is customary in population dynamics studies to present information on estimates of fecundity. In triclads, these are normally obtained by measuring cocoon production of individuals in the laboratory, and relating this to information obtained on the number of hatchlings from cocoons collected from the field and incubated in the laboratory (Reynoldson 1977). Unfortunately this proved impossible, since animals collected in the field could not be maintained in the laboratory for sufficiently long periods to allow cocoon production to be estimated. Even after strict quarantining, all animals succumbed to fatal infections of the facultative protozoan parasite T. pyriformis (see Chapter 2). This problem has been encountered in previous studies, and has never been adequately solved (Wright 1968; Lock 1972a). No estimates were therefore obtained of cocoon production per individual.

Similar difficulties were encountered in attempting to estimate numbers of hatchlings per cocoon. Although animals collected in the field often produced cocoons shortly after they were returned to the laboratory, collecting cocoons directly from the field proved almost impossible. Indeed only two cocoons were ever recovered from field sampling, despite considerable effort. This problem has also been encountered in previous studies (e.g. Lock 1972a), and relates to the fact mentioned previously that C.alpina deposits its cocoons in crevices in the substratum. Of the two cocoons collected, one was secreted inside the pupal case of a caddis fly and the other was found deep in a crevice of a stone removed from the stream bed.

Observations on sexual reproduction, therefore, were largely concerned with the occurrence and abundance of sexual individuals in the population at various stations throughout the year, and the relationship between size and sexual maturity.

The samples collected for the purposes of analysing population size structure were also utilised in assessing various aspects of reproduction within the population studied. The methods involved in collecting these samples have already been described in the previous section.

In these samples, sexually reproducing animals could be distinguished by the fact that they possessed a distinct copulatory complex (see above), which was absent in both immature and asexual individuals (but see later). In preliminary sampling, it was noticed that the degree of prominence of the copulatory complex was related to the extent of sexual maturation. Animals with ripe ovaries and mature sperm (observed by histological analysis)

## FIGURE 29

### Diagram illustrating the 'reproductive types' of C.alpina present in monthly samples

### SEXUAL

M = mature
PM = partially mature

In the partially mature animal, ___ denotes the underdeveloped copulatory bursa (labelled 'cb')

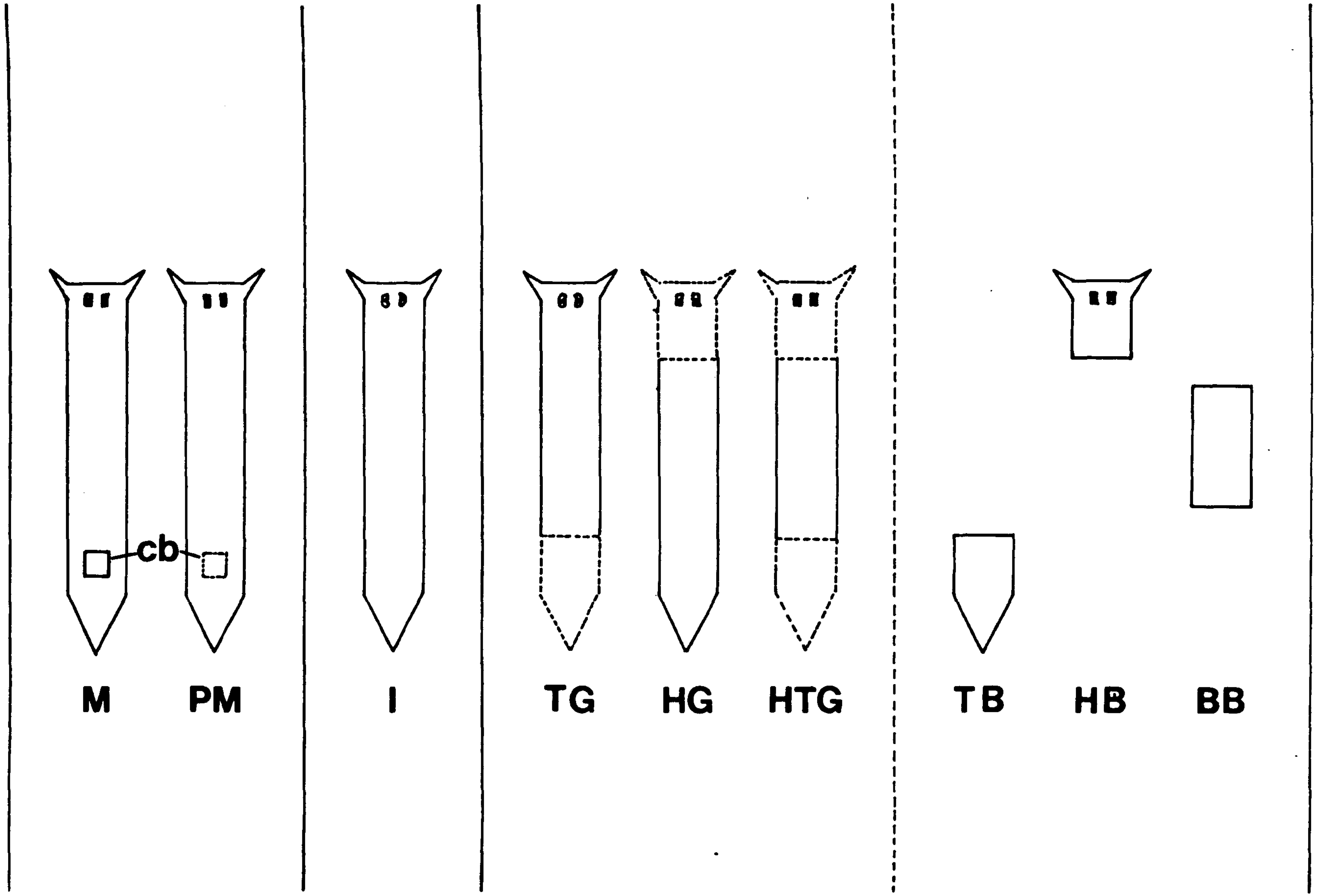
### IMMATURE

I = immature

### ASEXUAL

(i) 'growers' - TG = tail grower
HG = head grower
HTG = head-tail-grower
(ii) 'buds' - TB = tailbud
HB = headbud
BB = bodybud

In the asexuals ___ denotes parts of the body which have regenerated, but not repigmented.


cb
M
PM
I
TG
HG
HTG
TB
HB
BB

SAMPLING STATIONS

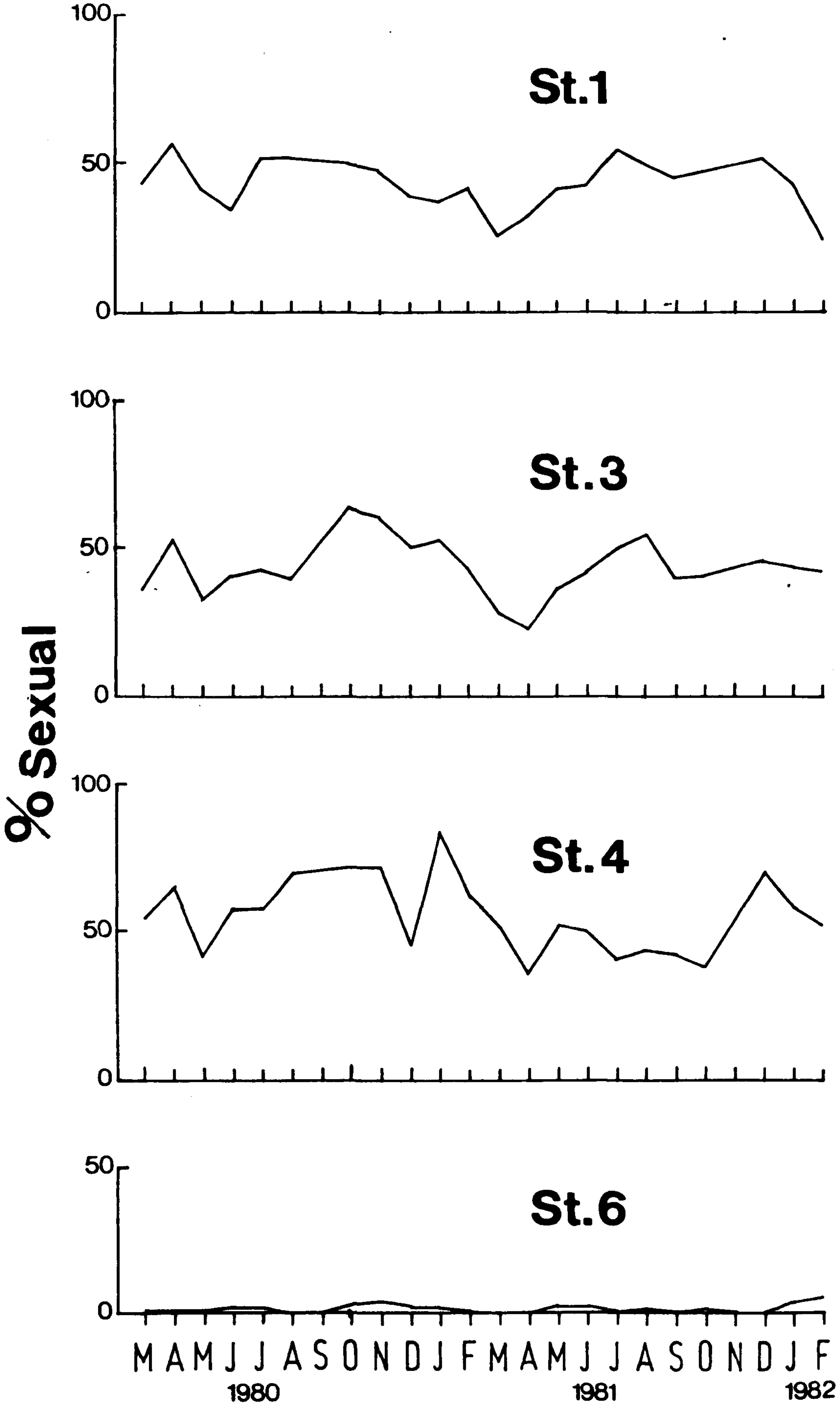
| | 1 | | | 3 | | | 4 | | | 6 | | | 7 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | PM | M | S | PM | M | S | PM | M | S | PM | M | S | PM | M | S |
| 1980 | | | | | | | | | | | | | | | |
| MAR | 14 | 30 | 44 | 2 | 35 | 37 | 15 | 40 | 55 | 1 | 0 | 1 | | ** | |
| APR | 14 | 43 | 57 | 15 | 38 | 53 | 11 | 54 | 65 | 1 | 0 | 1 | | ** | |
| MAY | 5 | 37 | 42 | 2 | 30 | 33 | 20 | 22 | 42 | 1 | 0 | 1 | | ** | |
| JUN | 9 | 26 | 35 | 16 | 25 | 41 | 16 | 42 | 58 | 0 | 2 | 2 | 1 | 0 | 1 |
| JUL | 10 | 42 | 52 | 14 | 28 | 42 | 14 | 44 | 58 | 1 | 1 | 2 | 6 | 4 | 10 |
| AUG | 11 | 41 | 52 | 10 | 30 | 40 | 14 | 56 | 70 | 0 | 0 | 0 | 0 | 6 | 6 |
| SEP | | ** | | | ** | | | ** | | | ** | | | ** | |
| OCT | 2 | 48 | 50 | 10 | 54 | 64 | 2 | 70 | 72 | 2 | 2 | 4 | 2 | 6 | 8 |
| NOV | 12 | 36 | 48 | 10 | 50 | 60 | 22 | 50 | 72 | 2 | 2 | 4 | 4 | 4 | 8 |
| DEC | 4 | 36 | 40 | 2 | 48 | 50 | 10 | 36 | 46 | 1 | 1 | 2 | | ** | |
| 1981 | | | | | | | | | | | | | | | |
| JAN | 4 | 34 | 38 | 15 | 38 | 53 | 36 | 48 | 84 | 0 | 2 | 2 | 8 | 5 | 13 |
| FEB | 8 | 34 | 42 | 15 | 28 | 43 | 26 | 36 | 62 | 0 | 1 | 1 | 1 | 12 | 13 |
| MAR | 10 | 17 | 27 | 9 | 20 | 29 | 10 | 42 | 52 | 0 | 0 | 0 | 2 | 7 | 9 |
| APR | 4 | 29 | 33 | 7 | 16 | 23 | 16 | 20 | 36 | 0 | 0 | 0 | 3 | 2 | 5 |
| MAY | 6 | 36 | 42 | 6 | 31 | 37 | 10 | 42 | 52 | 0 | 2 | 2 | 0 | 4 | 4 |
| JUN | 9 | 34 | 43 | 15 | 27 | 42 | 10 | 40 | 50 | 1 | 1 | 2 | 3 | 4 | 7 |
| JUL | 11 | 44 | 55 | 12 | 38 | 50 | 10 | 30 | 40 | 0 | 0 | 0 | 0 | 7 | 7 |
| AUG | 14 | 36 | 50 | 24 | 31 | 55 | 14 | 30 | 44 | 0 | 1 | 1 | 5 | 7 | 12 |
| SEP | 8 | 38 | 46 | 6 | 34 | 40 | 6 | 36 | 42 | 0 | 0 | 0 | 10 | 14 | 24 |
| OCT | 20 | 28 | 48 | 7 | 34 | 41 | 10 | 28 | 38 | 0 | 1 | 1 | 6 | 38 | 44 |
| NOV | | ** | | | ** | | | ** | | | ** | | | ** | |
| DEC | 16 | 36 | 52 | 19 | 27 | 46 | 28 | 42 | 70 | | ** | | | ** | |
| 1982 | | | | | | | | | | | | | | | |
| JAN | 16 | 28 | 44 | 10 | 34 | 44 | 12 | 46 | 58 | 1 | 3 | 4 | 2 | 12 | 14 |
| FEB | 6 | 18 | 24 | 14 | 28 | 42 | 22 | 30 | 52 | 1 | 5 | 6 | | ** | |

N.B. ** = missing data

Table 27 : % 'partially mature' (PM), % 'mature' (M) and total % sexual animals (S = PM + M) in monthly samples from stations 1,3,4,6 and 7 over the period March '80 to February '82.

FIGURE 30

Level of sexual reproduction (measured as % of sexual animals in monthly samples) at stations 1,3,4 and 6 over the period March 1980 to February 1982.


St.1
St.3
St.4
St.6
% Sexual
100
50
0
100
50
0
100
50
0
50
0
M A M J J A S O N D J F M A M J J A S O N D J F
1980
1981
1982

tended to possess very conspicuous copulatory complexes, whereas in those animals in which the ovaries were either at an early stage of development or 'spent', the copulatory complex tended to be paler and less distinct. These two general 'types' were assigned the terms 'mature' and 'partially mature' respectively (similar to Wright's (1968) use of these terms, although his definition only correlates conspicuousness of the copulatory complex with degree of development of the copulatory apparatus), and are represented diagrammatically in the summary of reproductive types given in Figure 29. It should be noted, however, that the distinction made between these two types was liable to be rather blurred.

## Results

The number of mature and partially mature C.alpina collected in each monthly sample during the period March 1980 to February 1982, together with summed monthly totals (representing the total percentage of sexual individuals in the population) are given as percentages for each sampling station in Table 27. The monthly totals of sexual animals (expressed as a percentage of the total sample) are summarised in Figure 30 (data for station 7 are not included here, but are presented later in Section C). Again it can be seen that the difference between the upstream area (station 6) and the downstream area (stations 1,3 and 4) demonstrated previously in the density and size structure data is similarly reflected in the relative occurrence of sexual reproduction in both areas.

At the downstream stations (1,3 and 4), sexual individuals occurred in the population in considerable numbers throughout the year (range 24%-84%), whereas at the upstream station (station 6), sexual individuals were either present in low numbers or were absent (range 0%-6%).

In the downstream stations, there was some evidence to suggest that the numbers of sexual individuals in the population varied seasonally, with maxima in late summer and early autumn, and minima in spring. These seasonal trends were particularly noticeable in stations 1 and 3, but were less obvious in station 4. If these seasonal fluctuations reflected the effects of the sexual reproductive cycle described for this species by previous authors (e.g. Beauchamp, 1933) i.e. a process of maturation, sexual reproduction, cocoon deposition and subsequent de-maturation, each occurring at specific periods during the year, then this could be checked by considering the relative numbers of partially mature and mature animals occurring throughout the year. If such a cycle was occurring at these stations, then partially mature animals would constitute the dominant type (in terms of numbers) at the beginning and end of the seasonal cycle (representing, respectively, 'maturing' and 'spent' individuals), whereas 'mature' animals would predominate in the middle of the cycle (representing actively reproducing individuals). The relative numbers of each type collected during the period March 1980 to February 1982 are given in Table 27 for each of the downstream stations. From these data, it seems unlikely that any such 'seasonal cycle' (as defined above) is occurring at any of these sites, since the percentage of 'partially mature' animals remains relatively constant throughout the sampling period at all of the downstream stations. It can be concluded that although the intensity of sexual reproduction varied seasonally at the downstream stations (1,3 and 4), there was no evidence of any 'breeding season' limited to certain months of the year. Indeed, sexual individuals were observed to deposit viable cocoons when returned to the laboratory on a number of occasions, in both summer and winter.

Considering the stenothermic nature of the upstream habitat, the low numbers of sexual individuals present in samples from station 6 was surprising (the reasons for this are discussed in Section C). It should be emphasised, however, that this did not reflect the inability of individuals at these stations to reproduce sexually (as has been found in similar situations in the American species _Polycelis coronata_ (Kenk, 1973)) since, as in the downstream stations, individuals collected in monthly samples produced viable cocoons on return to the laboratory on a number of occasions. This was an important observation, since it lessened the possibility that the reason for the low level of sexual reproduction in the upstream area was due to cytogenetic factors within the population, and suggested that perhaps external factors in the habitat upstream were in some way acting to suppress sexual reproduction. Considering other differences which existed, both between the populations, and their respective habitats (described in Section A), this seemed likely, and the reasons for this are considered at length in Section C.

Finally, it is worth noting that the possession of sexual characteristics was associated with the attainment of a particular size in this population studied: All sexually mature animals were >5mm in length, no evidence of any sexual characters was apparent in animals <5mm in length; this was true for all stations studied. Animals <5mm were therefore considered as 'juveniles' for the purposes of this study.

### (c) Asexual Reproduction

In freshwater triclads, asexual reproduction (for the definition of this term as used here see Chapter 1) occurs in two forms: binary fission, in which animals divide into two pieces, and multiple fission, in which animals divide into three or more fragments.

Although, in general, multiple fission is less common than binary fission throughout the Tricladida, it does occur regularly in certain groups. In the planariid genus *Phagocata*, for example, it is a common method of reproduction, and normally occurs in response to unfavourable conditions (Kenk 1972). Individuals break up into a number of pieces, each of which forms a cyst. After a period of time, a small fully regenerated individual emerges from each cyst. This is in marked contrast to the occurrence of multiple fission in *Dugesia gonocephala*, in which the fragments produced do not regenerate (Pattee and Persat 1978). In this species, multiple fission seems to be a pathological response to unfavourable conditions. The process of fragmentation is, however, poorly understood, and therefore it is difficult to make any general comments concerning the ecological importance of this process in triclad life cycles.

Binary fission itself can occur in two forms: paratomy and architomy. Paratomy, which involves some degree of regeneration of fission products prior to separation, is extremely rare among freshwater triclad species. Indeed, the records of its occurrence (Zacharias 1886; Kennel 1888) remain unsubstantiated, although it is common in the rhabdocoels.

In architomy, fission occurs as an initial separation of the individual into two parts - referred to hereafter as the headbud and tailbud. This separation occurs transversely across a line known as the 'fission plane', normally situated posteriorly to the pharynx, and is accomplished by the animal anchoring itself to the substrate by its tail and moving forward, thus 'tearing' itself in two (Child 1915). Regeneration of these two 'fission products' occurs only after separation has occurred, and involves two cellular processes of morphogenesis: Epimorphosis and morphallaxis (defined below). The relative importance of these two processes differs markedly between the regenerating headbud and tailbud. Tailbuds regenerate primarily by morphallaxis (Neutwig 1978; but see also Kenk 1937), a process by which tissues are re-organised in order to reform the relatively more complex head region, with its associated sensory structures; no blastema is formed during this process. In contrast, headbuds reform the less complex tail region by a process of epimorphosis, involving the formation of a blastema of undifferentiated cells (the so-called neoblasts) which subsequently differentiate to form a new tail. Beveridge (1981) has described this process in detail for the species *P.felina*. He notes that over a range of temperatures (5-15C),. the time taken by a tailbud to regenerate a head and grow to a given size is approximately twice as long as the time taken for a headbud to regenerate a tail and grow to a similar size. He points out that although there is little evidence to suggest that the process of head regeneration is any more costly than tail regeneration in energy terms (the growth and respiration rates of both fission products appear similar), the reason for the greater developmental time shown by tailbuds to reach a given size relates directly to the fact that headbuds are generally twice as large as tailbuds immediately after fission. In a recent paper arising from this work, Calow et al. (1979) have shown that in order to maximise fitness, species like *P.felina* which reproduce by fission should divert equal amounts of resources towards headbuds and tailbuds. i.e. the fission plane should be positioned in order to produce a division into two equal parts. The fact that the fission plane in *P.felina* is positioned to give a roughly 2:1 ratio of resource distribution between headbud and tailbud respectively is indicative of other selective forces acting to move the fission plane 'tailwards'. Beveridge (1981) noted that the survivorship of tailbuds under varying flow conditions (*P.felina* normally occupies lotic habitats) was size-dependent, and that large tailbuds were more susceptible to the actions of flow rate, and also that, in general, headbuds were less prone to dislodgement than tailbuds. In a recent study, it has been shown that populations of this species which occupy lentic habitats show greater variation in the position of the fission plane, and a 1:1 distribution of resources between headbud and tailbud is more common (Baird and Beveridge, in prep - reported in Sibly and Calow (1982)). Thus strong evidence exists to suggest that the distribution of resources between head and tail during fission can be influenced by selective forces in the environment. Further laboratory work is required, however, in order to understand the internal constraints operating on this process e.g. the energetic costs of the cellular processes involved in regeneration.

Asexual reproduction was first described in C.alpina by Dalyell (1853); in this and subsequent studies, it seems that asexual reproduction occurred solely by architomous fission, with the fission plane situated posterior to the pharynx. In his work on European populations of C.alpina, Steinmann (1907) considered asexual reproduction to be a pathological response to unfavourable temperature conditions, and that it was of secondary importance in comparison with sexual reproduction. Vandel (1921) disputed these findings, showing that asexual reproduction was a common process of true reproduction, and claimed that every individual was capable of both forms of reproduction, although they were temporally mutually exclusive. He also stated that the occurrence of asexual reproduction in an individual related to an indeterminate state of cellular differentiation, and was controlled by other environmental and hereditary factors, in addition to temperature.

Asexual reproduction is apparently common in British populations of C.alpina (Carpenter 1928; Wright 1968), and is normally associated with higher temperatures found in 'eurythermal' habitats in summer. This relates to the fact, mentioned earlier in this section, that the so-called 'stenothermic' nature of this species is believed to have a serious influence on its ability to reproduce sexually above certain temperatures. Wright (1968) claims that asexuality arose in C.alpina as an evolutionary response to the changing conditions which the species experienced following the last Ice Age. He speculates that during the Ice Age, C.alpina existed as a strictly sexual species, occupying stenothermic habitats. As the glaciers retreated, and the temperature regimes of these habitats at lower altitudes became increasingly eurythermal, the resulting high summer temperatures acted to physiologically inhibit sexual reproduction. Populations which were capable of asexual reproduction (presumably arising through mutation) in summer and sexual reproduction in winter would therefore be at an advantage, he claimed, and would predominate in such locations. Finally, populations limited to asexual reproduction would arise, since "asexual reproduction leads to aneuploidy which makes sexual reproduction increasingly difficult", though he fails to explain the reason for this.

In his work on a number of Welsh populations of C.alpina, Wright found what he called an "evolutionary sequence of reproductive type" i.e. sexual populations occurred at high altitudes and stenothermic sites, sexual/asexual populations occurred at intermediate altitudes in eurythermal sites and asexual populations occurred at low altitudes in eurythermal sites.

Dahm (1958) had previously carried out laboratory studies on these three 'reproductive types' in situations of varying temperature and ration level. He found that in populations exhibiting both sexual and asexual reproduction, the latter occurred exclusively at high temperatures, and at low temperatures was associated with low ration levels. Also, he found that sexuality could be induced in populations normally exhibiting only asexual reproduction in the field, by culturing individuals at high ration levels. In this case, however, non-viable cocoons were produced. He also analysed the three 'reproductive types' in terms of their karyology, finding that there was some evidence to suggest that asexual reproduction was linked with chromosome numbers other than tetra- or hexaploid counts, although the general difficulty he encountered in obtaining accurate counts from this species call even these tentative results into doubt.

The results from Dahm's studies, therefore, seem to favour the general outline of Wright's hypothesis, however further evidence is required in order to establish its validity.

Again, as in the case of sexual reproduction described earlier, temperature has been favoured by most studies as the major influence on the occurrence of asexual reproduction in C.alpina. In this case, the evidence linking asexual reproduction with 'high' temperatures is indirect (i.e. it is based on the absence of sexual reproduction at 'high' temperatures), and so the arguments are even less convincing than before.

There is, however, direct evidence to suggest that asexual reproduction is favoured in conditions of low resource availability. Dahm (1958) has shown that this can be demonstrated in laboratory experiments (see above), and Wright (1968) has commented on the fact that in field populations, intense intraspecific competition for food may reduce net availability of food per triclad, and may inhibit sexual reproduction. In such a situation, the low net resource availability would possibly favour asexual reproduction (Calow et al. 1979; Sibly and Calow 1982). Wright recognised, however, that further evidence from field manipulation experiments was necessary to test this hypothesis (see Section C).

In this section, the occurrence of asexual reproduction within the population of C.alpina being studied is analysed and commented upon, with particular emphasis being placed upon the nature of the fission process. Evidence is also presented on the occurrence of multiple fission within this population.

## Methods

Earlier in this section, the problems encountered in obtaining field and laboratory estimates of fecundity (in terms of cocoon production) were discussed. Problems of a similar nature were encountered in obtaining information on the contribution of asexual reproduction to population growth within the study area. In previous studies (e.g. Armstrong 1964), such information has normally been obtained from observations on the effects of temperature and ration level on laboratory cultures. Although this approach was attempted, difficulties involved in setting up such cultures proved insurmountable, due to the occurrence of lethal infestations of the protozoan parasite T.pyriformis (see earlier).

The information presented here on asexual reproduction is based on material collected in monthly samples over the period March 1980 to February 1982 (a description of the techniques involved in collecting these samples is given in the previous section). As with the data collected on sexual reproduction considered earlier in this section, analysis of the data on asexual reproduction was largely concerned with identifying the nature of the fission process, and establishing its duration and intensity over the study period at all stations sampled.

In C.alpina populations, asexual individuals can be readily identified, since the effects of recent fission and regeneration are easily recognised. Two basic 'types' of individual can be distinguished visually, relating to different stages of the regenerative process, and are referred to here as 'buds' and 'growers'. 'Buds', or more specifically 'headbuds' and 'tailbuds' are the individual products of fission, and are characteristically at an early stage of development (in terms of the regenerative process i.e. no blastema is visible). 'Growers' are defined as individuals in which regeneration of the body form has occurred, to a greater or lesser degree. More specifically, 'head growers' is the term used to describe a tail which is in the advanced stages of growing a head (i.e. the 'head' region is clearly distinguishable); 'tail growers' refers correspondingly to a head which is in the advanced stages of growing a tail. The second, 'grower', type is recognisable even at very advanced stages of regeneration, since when the 'body form' has been completely regenerated, the regrown tissue remains unpigmented for a considerable period afterwards. These terms correspond directly to the terms given by Beveridge (1981) to describe the products of asexual reproduction in P.felina, although the nomenclature differs slightly for reasons of clear definition.

In addition to the process of binary fission, which is the only method of asexual reproduction noted for this species in previous studies, it became obvious that this population of C.alpina was capable of multiple fission. The products of multiple fission could be clearly distinguished as two additional 'reproductive types' (see Figure 29): 'Buds' were observed in samples which were derived from the middle portion of intact animals i.e. they possessed neither of the characteristics of 'headbuds' or 'tailbuds' - these were referred to as 'bodybuds'. The second type was a 'grower' which exhibited a characteristic pattern of unpigmented head and tail regions, thus indicating that it was a regrowing 'bodybud' - these were referred to as 'head-tail-growers'.

The occurrence of multiple fission had never been recorded previously in this species, nor, indeed, in any of the other British species of triclad known to reproduce asexually. Absolute confirmation of the existence of this process was obtained when a number of animals underwent multiple fission in laboratory cultures. Regeneration of all of the products of multiple fission in these individuals indicated that this was not likely to be a 'pathological phenomenon' as had been described in D.gonocephala by Pattee (1978), neither did the fragments encyst, as had been noted for the genus Phagocata (Kenk 1973). Indeed, it seemed that multiple fission was a normal method of asexual reproduction, and its occurrence at the various stations sampled during the study period is described below.

One further asexual 'type' which undoubtedly occurred in samples throughout the study population was the recently regenerated individual in which pigmentation had returned to the regenerated body tissues. Unfortunately, these individuals proved indistinguishable from immature sexual animals (i.e. those with no obvious copulatory complex - see earlier) and from 'juvenile' individuals. These three indistinguishable forms were, by necessity, considered as one major group - the 'immature'

|  | SAMPLING STATIONS |  |  |  |  |
|---|---|---|---|---|---|
|  | 1 | 3 | 4 | 6 | 7 |
| 1980 |  |  |  |  |  |
| MAR | 13 | 41 | 26 | 30 | ** |
| APR | 10 | 23 | 16 | 69 | ** |
| MAY | 24 | 37 | 24 | 28 | ** |
| JUN | 19 | 20 | 13 | 12 | 34 |
| JUL | 18 | 12 | 8 | 24 | 22 |
| AUG | 15 | 24 | 2 | 23 | 28 |
| SEP | ** | ** | ** | ** | ** |
| OCT | 12 | 4 | 6 | 14 | 16 |
| NOV | 8 | 10 | 10 | 16 | 44 |
| DEC | 2 | 4 | 22 | 3 | ** |
| 1981 |  |  |  |  |  |
| JAN | 8 | 9 | 4 | 42 | 31 |
| FEB | 10 | 12 | 6 | 26 | 25 |
| MAR | 19 | 18 | 6 | 27 | 18 |
| APR | 11 | 14 | 12 | 22 | 19 |
| MAY | 16 | 8 | 4 | 9 | 21 |
| JUN | 10 | 8 | 2 | 6 | 14 |
| JUL | 14 | 11 | 4 | 10 | 19 |
| AUG | 13 | 8 | 10 | 18 | 20 |
| SEP | 13 | 14 | 8 | 12 | 18 |
| OCT | 8 | 9 | 10 | 20 | 22 |
| NOV | ** | ** | ** | ** | ** |
| DEC | 12 | 8 | 0 | ** | ** |
| 1982 |  |  |  |  |  |
| JAN | 10 | 11 | 8 | 16 | 26 |
| FEB | 4 | 13 | 12 | 11 | ** |

Table 28 : % Asexual animals in monthly samples at stations 1,3 4,6 and 7 during the period March 1980 to February 1982.

# FIGURE 31

Level of asexual reproduction (measured as % of asexual animals in monthly samples) at stations 1,3,4,6 and 7 over the period March 1980 to February 1982.

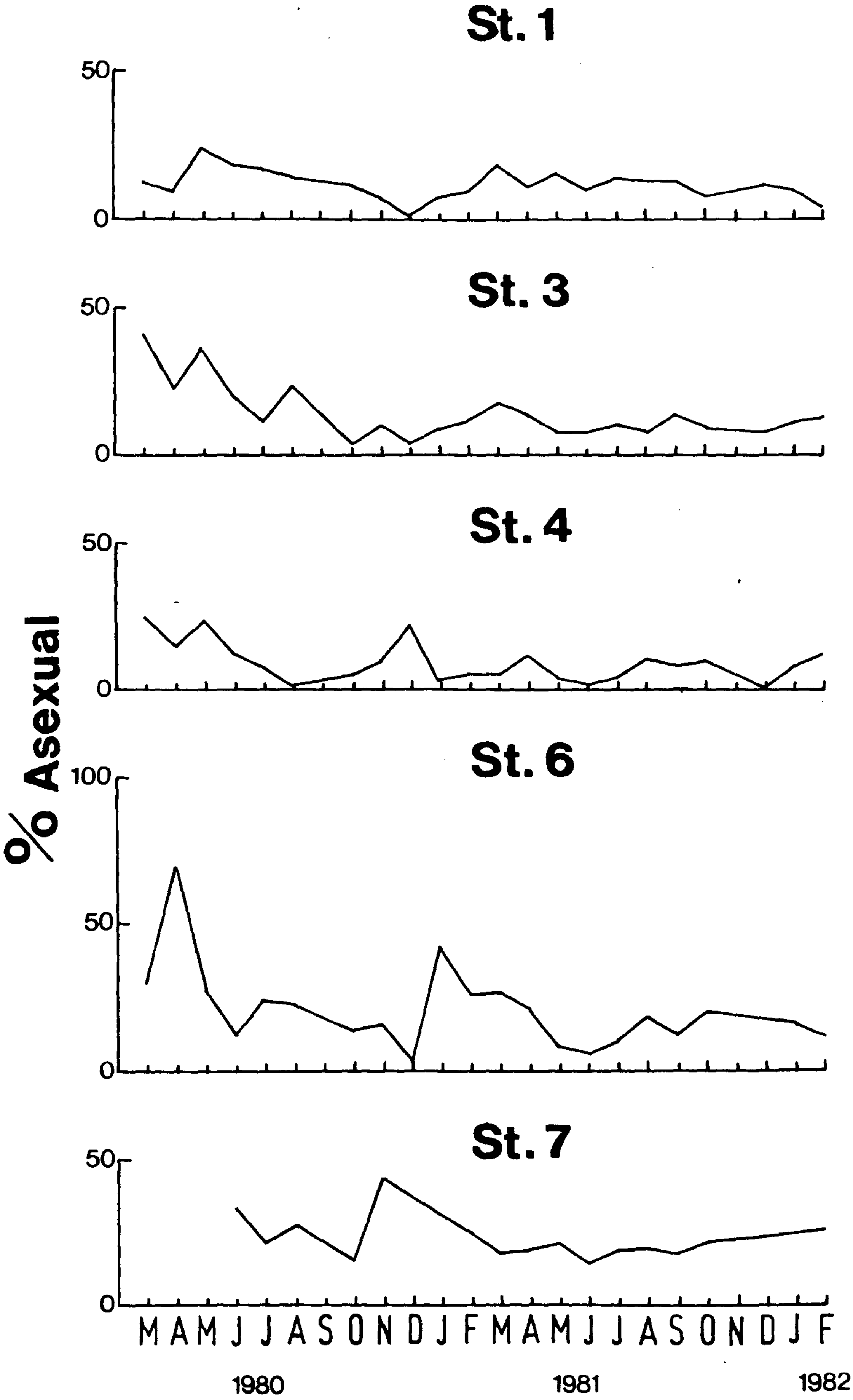
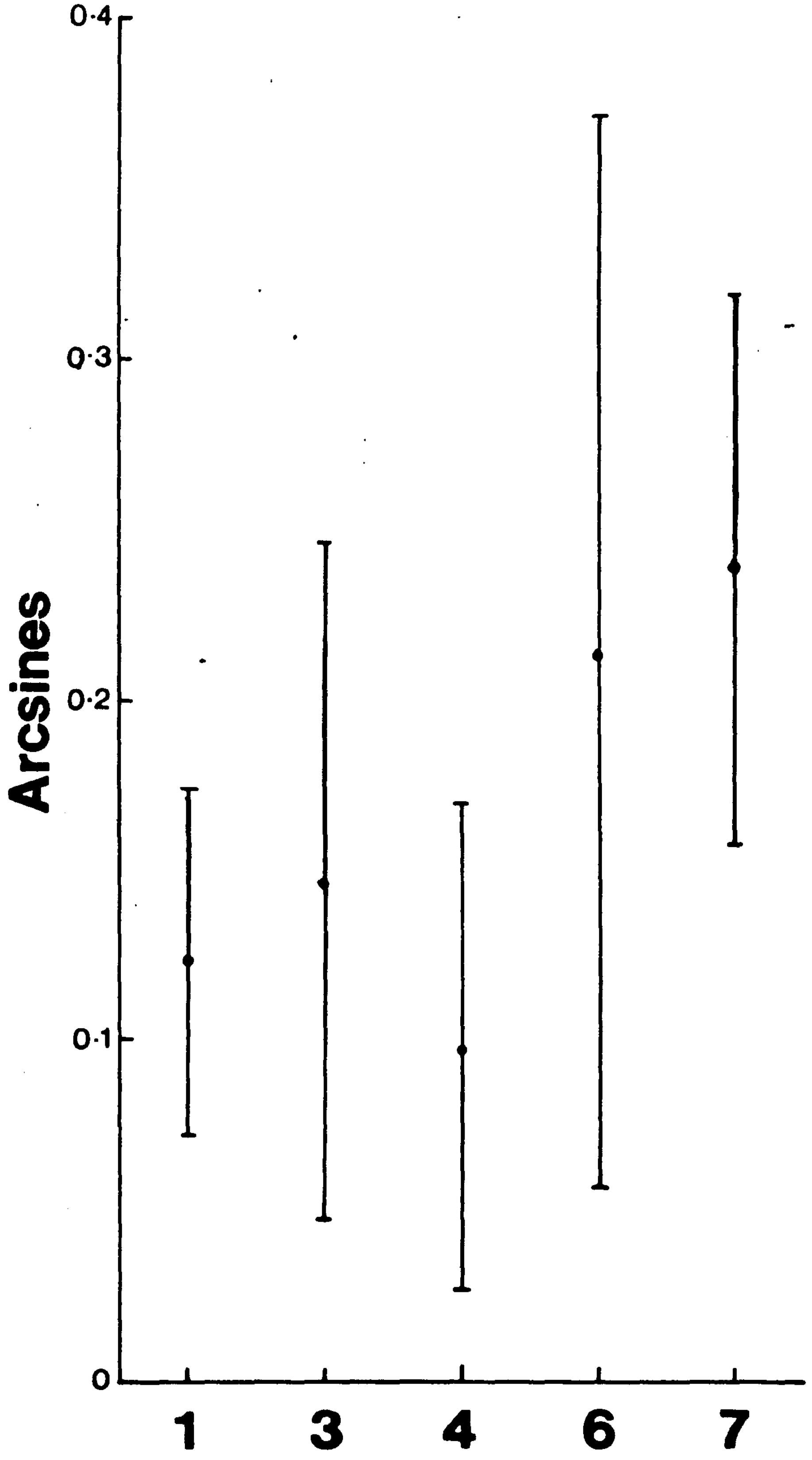

St. 1
50
0
St. 3
50
0
St. 4
50
0
% Asexual
St. 6
100
50
0
St. 7
50
0
M A M J J A S O N D J F M A M J J A S O N D J F
1980
1981
1982

FIGURE 32

Mean level of asexual reproduction at stations 1,3,4,6 and 7 (±95% C.L.) expressed as arcsines, calculated from the data in Table 28.


Arcsines
0·4
0·3
0·2
0·1
0
1
3
4
6
7

individuals. Their occurrence in samples collected is discussed briefly later in this section.

A diagrammatic representation of the six asexual categories described above is given in Figure 29.

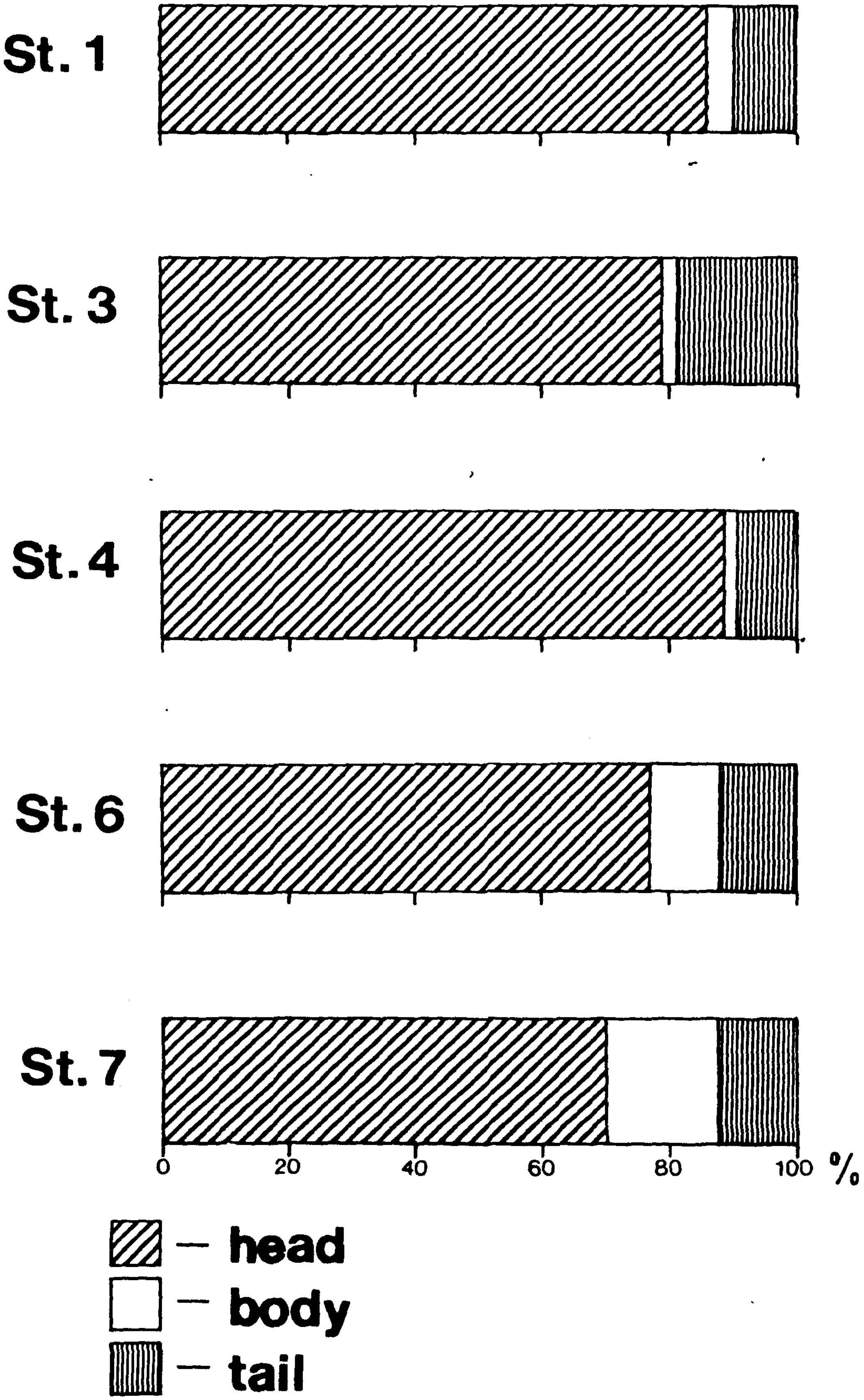
Results

The total numbers of asexual individuals collected at each station over the period March 1980 to February 1982 are given in Table 28 (expressed as a percentage of the total sample). Since these values do not contain those asexual animals which were assigned to the 'immature' group (see end of this section ), they necessarily underestimate the level of asexual reproduction at all stations. These results are summarised in Figure 31.

From these results, it was apparent that asexual reproduction was occurring throughout the year at detectable levels at all stations. Again differences existed between the upstream area (stations 6 and 7) and the downstream area (stations 1,3 and 4). If the mean level of asexual reproduction at each station is calculated together with 95% confidence limits (calculated from an arcsine transformation of the data), it can be seen that although there are some differences between stations in terms of level of asexual reproduction, these are not highly significant (presented in Figure 32). The differences existing between the two areas in terms of level of asexual reproduction were obviously much less distinct than those described earlier for sexual reproduction.

## FIGURE 33

% composition of asexual material from stations 1,3,4,6 and 7 in terms of whether head-, body- or tail-derived calculated from pooled monthly data


St. 1
St. 3
St. 4
St. 6
St. 7
0
20
40
60
80
100
%
— head
— body
— tail

Variation in the level of asexual reproduction within stations shows no particular seasonal pattern at any of the stations sampled. The results given in Figure 31 suggest that asexual reproduction was occurring at a fairly constant level throughout the year.

The totals given in Table 28 for the occurrence of asexual individuals at all five stations can be broken down into their individual categories according to whether they are derived from 'head', 'tail' or 'body' as summarised below:

HEAD = total no. of headbuds + total no. of tailgrowers
TAIL = total no. of tailbuds + total no. of headgrowers
BODY = total no. of bodybuds + total no. of head-and-tailgrowers

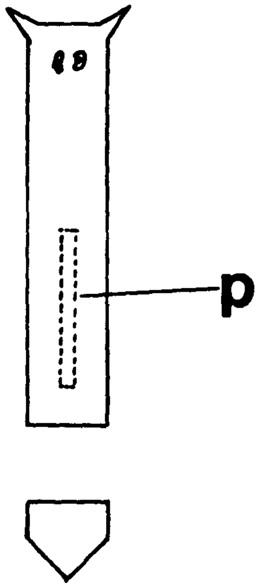
By grouping the data in this way it was possible to comment on the the relative survivorship of 'head', 'body' and 'tail' derived individuals, and also to obtain an estimate of the level of occurrence of multiple fission at each station.

The resulting categories were pooled for the period March 1980 to February 1982 for all stations. The relative occurrence of 'heads', 'tails' and 'bodies' in samples throughout this period are summarised in Figure 33. At all stations sampled, 'heads' constituted the major part of the asexual material. 'Tails' and 'bodies' were generally much more scarce, particularly at stations 1 and 4 on the downstream area. During the course of similar work on an asexually reproducing population of <u>P.felina</u> (which reproduced by binary fission only), Beveridge (1981) noted that 'heads' were normally more abundant in the field than 'tails' and suggested that this possibly related to the operation of a differential mortality factor, namely spate conditions, to which 'tails' were more susceptible than 'heads'. This hypothesis was not borne out by laboratory investigations, however, and the situation remained unexplained.

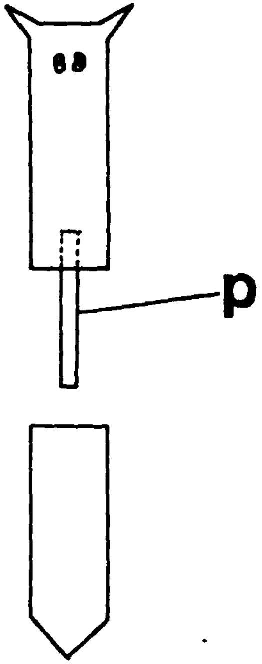
In this study no attempt was made to assess the relative susceptibility of the 'head', 'body' and 'tail' groups to high flow rates (although the evidence presented in the next section indicates that flow was apparently much less important as a mortality factor here, than in P.felina). However, there is some evidence from Figure 33 to suggest that 'body' types are more abundant upstream (stations 6 and 7) than downstream (stations 1,3 and 4). There are two possible explanations for this: Firstly, it is possible that a mortality factor is operating in the downstream area which particularly selects against 'body' types (e.g. flow rate). Secondly, it should be noted that the total number of 'body' types gives a minimum estimate of the occurrence of multiple fission at each site, and therefore this result may indicate that the upstream area is a more favourable environment for this strategy as opposed to binary fission. Clearly, these two explanations are linked, and receive further consideration in Section C.

It should be stressed that the occurrence of multiple fission within this population generally complicated the analysis of asexual reproduction. This was particularly

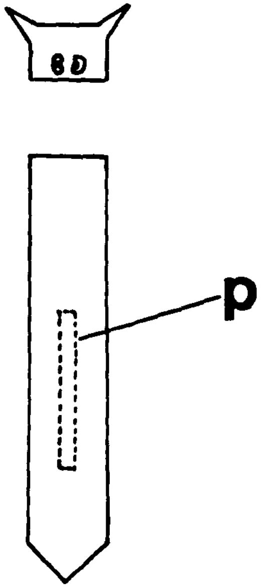
Fission below pharynx



Fission through pharynx



Fission above pharynx



apparent when considering the mechanisms of fission: It was not possible to determine whether or not 'tail' or 'head' types were produced as a result of binary or multiple fission. This meant that any analysis of the position of the fission plane (in relation to binary fission) in this species, such as had been carried out previously on P.felina by Beveridge (1981) and Baird and Beveridge (in prep.), would be open to question. For this reason, it was not possible to obtain quantitative details of the occurrence of various 'fission plane types' as had been given in the studies mentioned above. However, a critical analysis of the field material, together with a limited number of laboratory observations, tended to suggest that the position of the fission plane in this species-population was highly variable. Individuals observed which had recently fissioned (in field samples), and the few fissioning animals observed in the laboratory both indicated that fissioning above and through the pharynx was common, although fissioning below the pharynx was generally the most common method observed. A variety of fissioning types is presented in Figure 34.

A number of further observations were made, relating to the position of the fission plane in this population: Calow et al. (1979) comment on the fact that in P.felina, the normal result of fission is to produce a large 'head' and small 'tail'. They mention the possibility that animals may have been unable to fission 'through the pharynx', thus producing a 'head' and 'tail' of equal size, because this would have left each fission product with an incomplete pharynx. This is not a constraint in

C.alpina since the 'head' retains the whole pharynx, which can be observed trailing behind the 'headbud' following fission (see Figure 34).

It was also noted that 'heads' seemed more active than 'tails'; this was apparent even in the products derived from pre-pharyngeal fission (see Figure 34), when 'tails', despite their large relative size, tended to move sluggishly, whereas 'heads', even though they constituted virtually only 'eyes and head tentacles', were observed to move rapidly. This is presumably related to the fact that the 'heads', by retaining the sensory apparatus, were able to react to enviropnmental stimuli (e.g. light), whereas the 'tails' were not. This may be an important factor in determining the relative survivorship of 'heads' and 'tails' in the field, since the possession of sensory apparatus by 'heads' would, for example, allow them to retain the ability to detect alterations in flow rate.

### (d) Immature Animals

The occurrence of animals possessing no apparent reproductive characteristics proved a complicating factor in interpreting the monthly samples. Since it was impossible to assign these individuals to either the asexual category (since they showed no evidence of binary or multiple fission) or the sexual category (since they possessed no copulatory complex), a further category was adopted, which could have included three types of individual (although these were visually indistinguishable):

(i) 'Asexual' animals which had either regenerated completely (i.e. tissues had repigmented) or were about to fission.

(ii) 'Sexual' animals which were at an early stage of sexual development.

(iii) 'Juvenile' animals which had recently hatched from cocoons (this class <5mm).

Obviously, it was not possible to assess the composition of the 'immature' animals collected at each station in terms of the relative quantities of these three types. It was therefore assumed that the 'immature' group of animals collected in samples at each station was probably composed of proportions of types (i) and (ii) (see above) in direct proportion to the levels of 'sexual' and 'asexual' reproduction estimated from the remainder of the sample at each station (i.e. the remainder being composed of distinguishable sexual and asexual animals). This group receives no further consideration in this study, although data on the total size-frequency distribution of immature animals at each station is given in Fig. 28.

### (e) General Discussion

In a study on a Welsh population of C.alpina which reproduced both sexually and asexually, Carpenter (1928) provided evidence to show that the relative proportions of sexual and asexual individuals in the population varied cyclically throughout an annual period, and that they were inversely proportional to each other. She showed that the level of sexual reproduction within the population peaked in winter and was subsequently depressed by increasing temperature. In contrast, the level of asexual reproduction within the population peaked in summer, and was promoted by increasing temperature. She concluded that the relative levels of sexual and asexual reproduction were controlled directly by habitat temperature. This has been proposed by a number of authors (see review of literature relating to sexual and asexual reproduction earlier in this Section), but Carpenter (ibid.) was the only one to provide hard data.

If the results given for the Fairy Loch population of C.alpina are examined in the light of this hypothesis, two important general observations emerge: Firstly, the data obtained in this study concerning sexual and asexual reproduction (Figs. 30 and 31 respectively) in relation to habitat temperature (Fig. 4), bear little resemblance to those obtained for a similar type of population (i.e. consisting of sexual and asexual individuals) by Carpenter (ibid.). Secondly, and more importantly, there was apparently no relationship between temperature and level of reproduction, whether sexual or asexual, and furthermore, no inverse relationship between the levels of sexual and asexual reproduction. However, the virtual absence of sexual reproduction from the upstream area (Fig. 30 - station 6), despite the fact that this was a 'stenothermic' habitat, and hence 'ideal' for sexual reproduction (as predicted from the hypothesis discussed in the literature review earlier in this Section), compared with the occurrence all-year-round of sexual reproduction in the 'eurythermic' downstream area (Fig.30 - stations 1,3 and 4), would suggest that in this population of C.alpina sexual reproduction was favoured in 'eurythermic' conditions, and inhibited in 'stenothermic' conditions. This result was a complete reversal of those from previous studies linking habitat temperature with the occurrence of sexual reproduction, and is irreconcilable with the hypothesis stated earlier, which was supported by Carpenter's evidence.

Clearly, a major re-examination of existing theory concerning the reproductive biology of this species is required in order to incorporate the results obtained in the present study. This is done in the following Section C, in which the results presented in this Section concerning the occurrence and intensity of sexual reproduction, population density and population size structure are discussed together with relevant information on the habitat occupied by C.alpina. By doing this, it has been possible to propose a new hypothesis to explain the relative occurrence of sexual and asexual reproduction in this species, which is tested by further experiments, the results of which are also presented and discussed therein.

### B(vi) : Mortality Factors

In recent studies on stream-dwelling triclad populations, two major causes of mortality have been identified: Dislodgement by high flow rates and predation (for references see Chapter 2). Both these factors are considered here, although it was beyond the scope of these investigations to give the latter any more than cursory attention.

(a) Flow Rate

Studies on the action of current flow on stream-dwelling triclad species have mostly been carried out in the laboratory, and have normally been employed in order to demonstrate interspecific interactions. Of the species studied, C.alpina is apparently most tolerant of high flow rates, and this is reflected indirectly in field observations (Wright 1968, 1974). The only attempt to assess the direct effects of flow rate on triclad populations in the field was carried out by Beveridge (1981) for the species P.felina. In his study, mortality was measured by counting the numbers of animals collected in drift samples, and correlating these results with flow rate measurements. Despite the fact that triclads commonly appeared in the drift, the correlation between triclad numbers collected and flow rate was surprisingly poor. However, it was noted that in these samples, the numbers of damaged animals generally correlated with high flow rates.

In this study, the drift samples collected at stations 3 and 6 over the period March 1981 to February 1982 described in Section A were used to assess the levels of triclads occurring in the drift. The methods involved, therefore, are described in detail in Section A, and were similar in most respects to those employed by Beveridge (ibid.) in the study mentioned above.

Over the period April 1981 to March 1982, only two triclads were recovered in total from twelve monthly drift samples at station 3, and only five triclads in total from similar samples collected at station 6 (results from Section A: Tables 20 and 21).

It seems then, that flow rate had little effect on the population of C.alpina at either station, even in conditions of spate.

It was concluded, therefore that dislodgement by current was probably less important as a mortality factor in field populations of C.alpina than had been reported for P.felina by Beveridge (1981), and that this was due to its ability to tolerate high flow rates (Wright 1968; 1974).

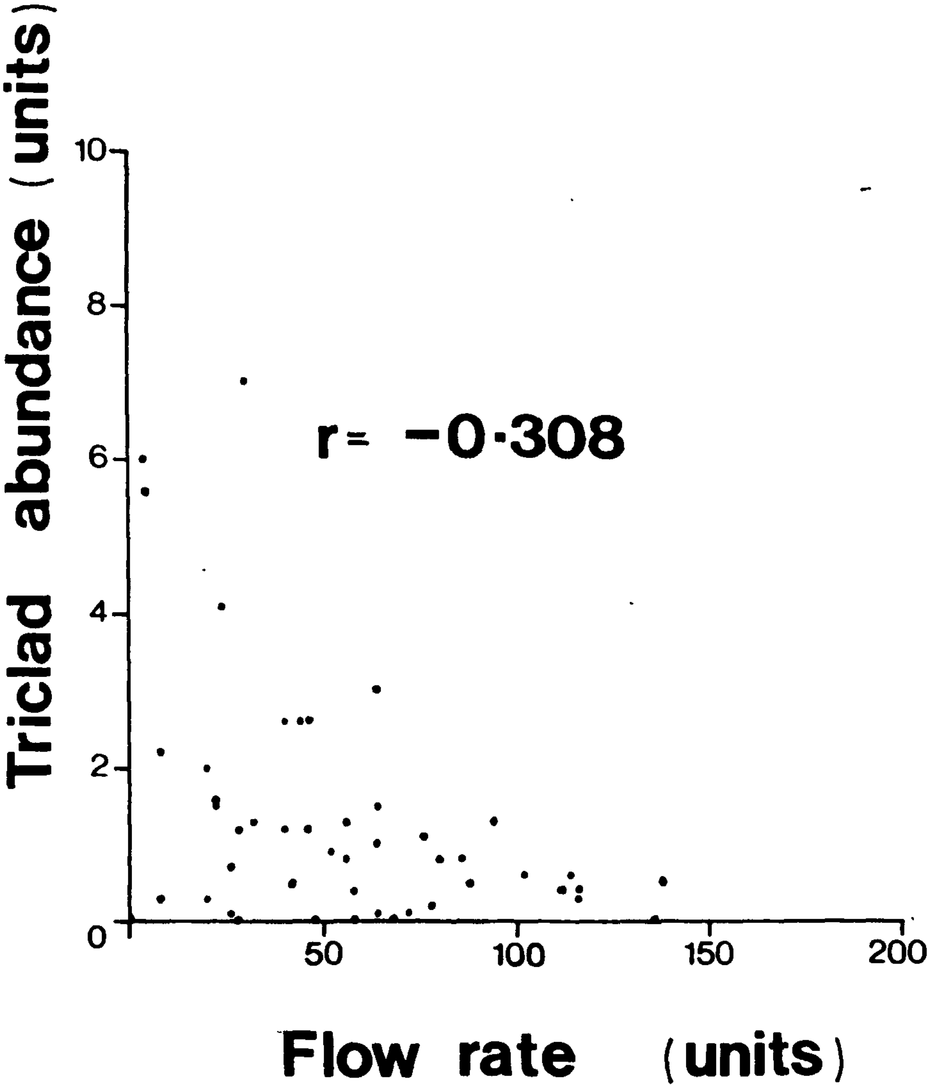
During the collection of density estimates, it was observed that C.alpina often occurred in aggregations of individuals, and that that these clumps tend to occur on stones lying in areas of low current flow. In order to test the possibility that C.alpina was able to avoid dislodgment by high flow rates, not only by its tolerance of such conditions, but also by actively seeking out and occupying areas of relatively quiet flow, an attempt was made to quantify the observations mentioned above.

A site approximately 10m. below station 4 was chosen, and an area of the stream bed approximately $3m^2$ was subdivided into 48 quadrats of equal area ($0.063m^2$). Within each quadrat, a flow reading was taken with an Ott current meter and the number of triclads within the quadrat was recorded. To correct for the fact that each quadrat enclosed different amounts of substrate (i.e.

FIGURE 35

Relationship between triclad abundance (for a definition of this term see text) and flow rate (measured as current meter units).

r = -0.308, significant at p = 0.05, 47d.f.


Triclad abundance (units)
10
8
6
4
2
0
r= -0·308
50
100
150
200
Flow rate (units)

stones), the numbers of triclads recorded in each quadrat was corrected to an 'abundance value' by dividing by the numbers of stones present. In this case only stones >30 mm. in diameter were considered, and no correction was made for surface area (as had been made in the density estimates discussed earlier in this Section).

The results are summarised as a scatter diagram in Figure 35. The correlation between flow rate (measured in 'current meter units') and triclad abundance was low ($r = -0.308$), but significant (at $p = 0.05$, 47df.). The high degree of scatter apparent in Fig. 35 presumably relates to the fact that stone size was highly variable in each quadrat and hence presumably influenced triclad density, and also to the fact that conditions other than flow rate were important in determining dispersion pattern e.g. food availability, presence of predators etc.

Finally, it should be emphasised that the results presented in Fig. 35 do not necessarily reflect the direct actions of current flow in this population. It is possible that aggregations of triclads may occur in areas of 'quiet' flow, not in order to avoid high flow rates, but to exploit the drift material which probably constitutes the greater part of their diet. This drift material becomes trapped between stones and presumably accumulates at a higher rate in areas of quiet flow than in high flow areas, since these areas are generally subject to less physical disturbance. Further study is required on this.

| PREDATOR SPECIES | IMMOBILISED PREY ITEM | ACTIVE PREY ITEM |
|---|---|---|
| D.CEPHALOTES | *** | *** |
| I.GRAMMATICA | *** | *** |
| B.RISI | *** | DNF |
| P.FLAVOMACULATUS | *** | *** |
| R.DORSALIS | *** | DNF |

'***' denotes that feeding occurred

'DNF' denotes that the animal did not feed

Table 29 : Results of predation experiments - potential predator species presented with immobilised and active C.alpina.

### (b) Predation

In the previous Section, the occurrence of potential predators, previously reported to feed on C.alpina (for references see Chapter 2) was discussed, and the relative abundance of these species in the downstream and upstream stations considered. Although no serological studies were carried out, this section discusses a number of qualitative feeding experiments which were performed to test the assumption that predator species which occurred in the Fairy Loch system would readily feed on C.alpina.

The methodology of these experiments was simple: Samples of D.cephalotes, I.grammatica, P.flavomaculatus, R.dorsalis, and B.risi (see Section A) were placed in individual crystallising dishes containing filtered stream water. Active and immobilised (by squashing) potential prey items (C.alpina) were introduced in separate experiments, following which the dishes were placed in a 10C cold room for four hours. The experiments were observed at regular intervals over this period, and any evidence of feeding by the 'potential' predator species was noted. The results of these experiments are presented in Table 29.

From these results, it can be seen that all five predators fed readily on immobilised C.alpina, and D.cephalotes, I.grammatica and P.flavomaculatus also fed on active C.alpina. While this does not provide conclusive proof that these species feed on C.alpina in the field, there is nevertheless evidence that this was possible.

## Section C : General Discussion and Further Experiments

### C(i) : Introduction

It is evident from a close examination of the literature on C.alpina that despite considerable research effort, the influence of abiotic and biotic environmental factors on the distribution and abundance of this species is poorly understood. This is particularly true in the effects of these factors on the reproductive ecology of this species. Reproduction in populations of C.alpina is obviously a complex process, but despite this, field studies have concentrated almost exclusively on the influence of a single abiotic environmental factor (i.e. temperature) in their attempts to understand the interrelationship between sexual and asexual reproduction. In laboratory studies, and in particular the work of Dahm (1958), however, it has been demonstrated beyond all doubt that other factors, especially ration level (or resource availability), are of equal, if not greater importance in controlling reproduction. Despite the critical importance of Dahm's studies no attempt has yet been made to apply his results to a broader consideration of the reproductive ecology of C.alpina in the field, one in which the factors which influence resource availability, together with temperature are examined in relation to the processes of reproduction. (Although Wright (1968) comments on the reproductive ecology of this species, his work is mainly concerned with interrelationships between C.alpina and other stream-dwelling species).

In this study, the approach has been similar to that described above, and the results obtained, which until now have been considered in isolation, are discussed below in an attempt to relate the variations in abiotic and biotic factors existing in the habitat (described in Section A) with the differences observed within the population of C.alpina in distribution, abundance and, especially, reproduction. Following this, a hypothesis is presented to explain these results in relation to current ideas relating to the biology of this species. Finally, this hypothesis is tested by a field experiment and the results of this discussed; ideas for future work are also given.

## C(ii) : Discussion - The Effects of Habitat Variability on the Population

Of the eight sampling stations within the Fairy Loch system, only five actually contained triclads. The reasons for the absence of triclads from these habitats (stations 2, 5 and 8) has been discussed earlier and only the five stations (i.e. 1, 3, 4, 6 and 7) containing triclads will be considered.

These stations were grouped into two areas, initially relating to topographic differences, stations 1, 3 and 4 being referred to as 'the downstream area', and stations 6 and 7 as 'the upstream area'. The results presented in Section A however, showed that these two areas differed not only in topography, but also in temperature regime, flow conditions and in structural and functional aspects of the associated macroinvertebrate community. Indeed these two areas constituted two radically different habitats.

The downstream habitat exhibited a eurythermic temperature regime, which was influenced directly by ambient air temperature. Flow conditions in this area were variable, and the conditions of spate which occurred did so seasonally and related directly to the interaction between rainfall and gradient at each particular location along the length of the stream. The actions of flow in this habitat, particularly during spate conditions, had a profound effect on the nature of the substratum: In locations subject to generally high flow rates, the substratum was reduced to bedrock, whereas in the lower areas of flow, the substratum was composed of particles of a variety of sizes ranging from large boulders to gravel. There were no major permanent areas of 'silt', although smaller particles accumulated in areas of low flow during the summer months, when current flow was generally lower than at other times of year. The water chemistry of the Fairy Loch system was typical of that found in Scottish upland streams of a similar geology, with the low levels of dissolved organic material suggesting a habitat of particularly low productivity. The structure and function of the macroinvertebrate community in this habitat were greatly influenced by these abiotic factors, of which flow conditions had the more profound effect (but see above). In terms of numbers, the community in this habitat is generally dominated by 'collector' species, such as caseless caddis larvae, particularly in the higher flow areas. This relates to the fact that allochthonous material of large particle size (which, as leaf/twig packs, constitutes a substratum in addition to being a food resource (CPOM)) tends not to accumulate in such locations, and consequently the species which exploit this resource - the 'shredders' - are less abundant. This habitat can therefore be considered as an FPOM-powered system, in which the smaller particles of allochthonous material (resulting from detritus processing by shredders in the Fairy Loch community (station 5)) constitute the dominant detrital resource. Of the other two 'functional feeding groups' in the community, predators, including C.alpina, are common, where as 'scrapers', with the possible exception of A.fluviatilis, were scarce. The productivity of the habitat was not measured directly but drift was used as an indirect measure. Drift biomass apparently varied seasonally, for reasons relating to flow rate and other factors which were discussed earlier, showing a major peak in spring/summer and a minor peak in winter.

In summary, therefore, this habitat appeared to be highly seasonal in nature, with periods of high physical disturbance occurring in the autumn/winter half of the year, relating to the influence of rainfall on flow conditions.

The upstream habitat exhibited a stenothermic temperature regime, in which the water temperature in the stream was relatively 'low' in summer and relatively 'high' in winter, with respect to ambient air temperature, by the fact that a number of small springlets discharged into the stream at various locations along its length. In contrast to the downstream habitat, flow conditions in this area were less variable, and the almost 'flat' gradient over which the stream flowed resulted in a slower current prevailing throughout the year. Consequently, the substratum in this habitat was characterised by a smaller particle size than the downstream area, being composed of areas with stones on gravel and sand separated by large areas of deep silty deposits in locations of quiet flow. The water chemistry of this area was, however, similar to that of the downstream area, with low levels of DOM indicating a habitat of low productivity. Again, as in the downstream habitat, the prevailing flow conditions greatly influenced the structure of the macroinvertebrate community. In this habitat, however, the much lower order of flow allowed the build-up of leaf litter and other allochthonous detritus, and 'shredders', particularly Gammarus, constituted the dominant functional feeding group. 'Collectors' were less common than downstream, and this was particularly true of those species which relied on a constantly high average flow rate in order to obtain food e.g. net-spinning caddis larvae. With the notable exception of C.alpina, predators were also less common than in the downstream habitat, and again 'scrapers' were almost completely absent. The indirect measure of productivity by drift collection indicated that although drift biomass was slightly lower than downstream, the general seasonal pattern of a spring/summer major peak followed by a minor peak in winter was the same as in the upstream habitat. The winter peak however, was much less pronounced.

In contrast with the downstream habitat, therefore, the upstream habitat was much less seasonal in most major respects, with the possible exception of the seasonal variation in drift biomass. A general summary of the differences which existed between these two habitats is given in Table 30.

The difference between the two habitats relating to seasonality, described above, was reflected in the observations made on the populations of C.alpina inhabiting each area. The topographic nature of the Fairy Loch system, specifically the existence of physical barriers - namely the Fairy Loch itself and the steep gradient area around station 2 - which probably limited dispersal, allowed what was probably one original population to be divided into three isolated sub-populations: One occupying the downstream habitat below station 2, one occupying the downstream habitat above station 2, and a further population inhabiting the upstream habitat. For the purposes of this discussion, however, the two downstream 'sub-populations' were considered as a single group in order to simplify comparisons between the downstream and the upstream habitats. This was considered valid, since both these sub-populations occupied a similar habitat, and also exhibited general similarities in relation to population parameters described in Section B.

From the results given in Section B, it was noted that the downstream population of C.alpina exhibited obvious differences from the upstream population in a

| | DOWNSTREAM | UPSTREAM |
|---|---|---|
| ENVIRONMENTAL FACTORS | | |
| GRADIENT | steep | shallow |
| WATER CHEMISTRY | SIMILAR | |
| TEMPERATURE REGIME | eurythermic | stenothermic |
| FLOW RATE | high/variable | low/constant |
| DIVERSITY | high | low |
| DOMINANT FUNCTIONAL FEEDING GROUP | collectors | shredders |
| PRIMARY RESOURCE TYPE | FPOM | CPOM |
| ABUNDANCE OF PREDATORS OF TRICLADS | abundant | scarce |
| POPULATION PARAMETERS | | |
| DISTRIBUTION | continuous | sporadic |
| DENSITY | low | high |
| AVERAGE SIZE | large | small |
| SEXUAL REPRODUCTION | high | low |
| ASEXUAL REPRODUCTION | SIMILAR | |
| OCCURRENCE OF MULTIPLE FISSION | lower | higher |

N.B. the terms high/low etc. are used in a relative sense only.

Table 30 : A summary of the differences between the downstream and upstream habitats described in Section A, together with a summary of the differences between the populations of C.alpina from each area described in Section B.

number of characteristics.

The downstream population occurred at typically low density relative to the upstream population, and there was evidence to suggest that population density fluctuated seasonally with major peaks occurring in summer and a minor peak following in winter. In contrast, the population density in the upstream area remained relatively constant throughout the study period. Although it was not demonstrated statistically, there was strong evidence to suggest that the average size of animals in the downstream population was greater than animals in the upstream population. Differences also existed in the reproductive profile of the two populations: In the downstream population, sexual reproduction occurred at significant levels throughout the year, and there were indications that the level of sexual reproduction varied seasonally, with peaks occurring in summer/early autumn. Asexual reproduction also occurred at significant levels throughout the year, although in this case there was little evidence of a seasonal pattern in the level of its occurrence. In the upstream population, sexual reproduction was virtually absent throughout the study period. Asexual reproduction occurred at significant levels throughout the year, however, but as in the downstream population, there was little evidence of any predictable seasonal pattern in its level of occurrence. These differences are summarised in Table 30.

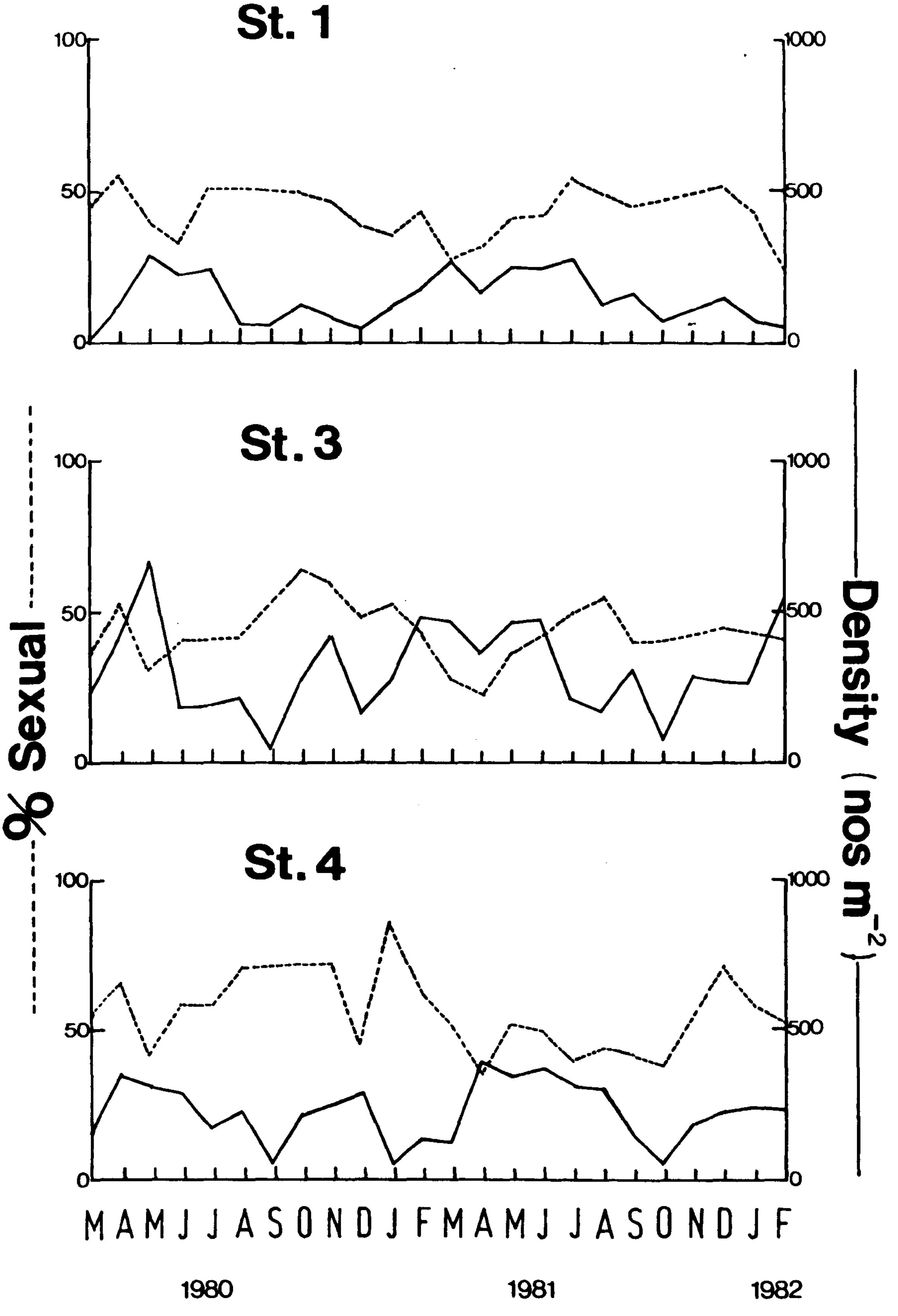
In the previous section, the hypothesis that the differences in level of sexual reproduction between the upstream and downstream populations related to differences in thermal conditions between the two habitats, was rejected. The reasons for this were discussed, and related to the fact that the results obtained in this study linking sexual reproduction with eurythermic conditions were a complete reversal of the results presented in previous studies, where sexual reproduction was linked with stenothermic conditions. It was suggested that a hypothesis which linked sexual reproduction with ration level (or, as in the field situation, resourcee availability) might prove more suitable, given the fact that this has been demonstrated in the laboratory (Dahm 1958).

Increased food availability has been shown, in the laboratory, to promote the development of sexual characteristics in C.alpina (Dahm ibid.). In field populations, resource availability per triclad depends directly on the total availability of resources within the habitat and the numbers of triclads competing for these resources. In otherwords, for a given level of resource availability within a habitat (i.e. productivity) the occurrence and level of sexual reproduction would depend on the total number of triclads present (i.e. the population density). If resources were scarce, intraspecific competition for food would intensify, and therefore net resource availability per individual triclad would decrease, consequently depressing the level of sexual reproduction within the population. Factors which act to control or limit density would therefore have an indirect effect on the occurrence of sexual reproduction e.g. mortality factors, such as predation (which is known to limit the distribution, and hence presumably the density, in field populations of C.alpina (Wright 1975)) could have such an effect, as could interspecific competition with other triclad species (Lock and Reynoldson 1976 - but see Chapter 2). In situations where net resource availability per triclad is sufficiently low to inhibit sexual reproduction in some or all individuals, there is evidence (Calow et al. 1979) that asexual reproduction would be increasingly favoured over sexual reproduction, due to the fact that the former is more efficient in converting resource input into reproductive output in situations of low resource availability.

The evidence presented in this study, based on observations of two populations of C.alpina exhibiting different reproductive strategies, strongly supports this hypothesis. It has been demonstrated that triclad density was considerably lower in the downstream habitat than in the upstream habitat. Although no direct estimates of productivity were obtained, indirect evidence suggested that resource availability in the two habitats was largely similar, and, if anything, was higher in the downstream habitat, particularly during spring/summer. Given these two results, the hypothesis stated above would predict that the downstream habitat would be more favourable for the occurrence of sexual reproduction than the upstream habitat, since the potential net resource availability per triclad would be greater; consequently, it would also predict that the average size of animals in the downstream population would be greater than those in the upstream

FIGURE 36

Data from Fig.21(density) and Fig.30(% sexual) combined to show the relationship between population density and level of sexual reproduction at stations 1,3 and 4 over the period March 1980 to February 1982


St. 1
St. 3
St. 4
100
50
0
1000
500
0
% Sexual
Density (nos $m^{-2}$)
M A M J J A S O N D J F M A M J J A S O N D J F
1980
1981
1982

population.

Clearly, the first prediction holds true for these populations, and the second prediction, although not statistically verified, is supported by strong evidence.

Further evidence supporting the hypothesis is presented in Fig.36, which shows that in the downstream stations, the seasonal variation in level of sexual reproduction was apparently inversely related to the seasonal variation in population density.

Having suggested a relationship between triclad density (and hence net resource availability per triclad) and the level of sexual reproduction within these two populations, the question arises: Why is the population density of C.alpina higher in the upstream habitat than in the downstream habitat? One possible explanation lies in the occurrence and intensity of the specific mortality factors considered in the previous section i.e. dislodgement of animals by current, and predation. Clearly, if these two factors are operating to cause mortality in the two populations, they are doing so at a much higher level in the downstream habitat, where predators are common and the flow rate is more variable and generally higher than in the upstream habitat. If this were so, the high population density occurring in the upstream habitat could possibly be explained by the fact that the relatively low level of operation of these factors within this area was failing to hold numbers down to the level exhibited by the downstream population. Evidence collected has indicated the doubtful nature of flow rate as a potential mortality factor, however, and despite strong supportative evidence, the status (as 'predators') of the five species, mentioned earlier, cannot be positively confirmed in the absence of serological studies similar to that described by Wright (1975), and therefore this question cannot be answered with certainty.

### C(iii) : Further Experiments

Reynoldson (1966), in discussing the occurrence of intraspecific competition in lake-dwelling triclad species, notes that it should be possible, by field manipulation experiments, to assess whether or not field populations of triclads are resource limited. These manipulation experiments could take two forms: One involving artificial increase of the available food supply, and the other involving artificially decreasing the density of the triclad population by removing individuals. The resulting increase in average size of the individuals in a resource limited population could be considered as good evidence for the occurrence of intraspecific competition.

These two techniques, which both manipulate the net resource availability per triclad, could both be employed in testing the hypothesis relating this factor with the occurrence of sexual reproduction. Clearly, if it could be demonstrated that a population exhibiting low levels of sexual reproduction could be induced, by reduction in density, to exhibit higher levels of sexual reproduction, then this would provide strong evidence for this

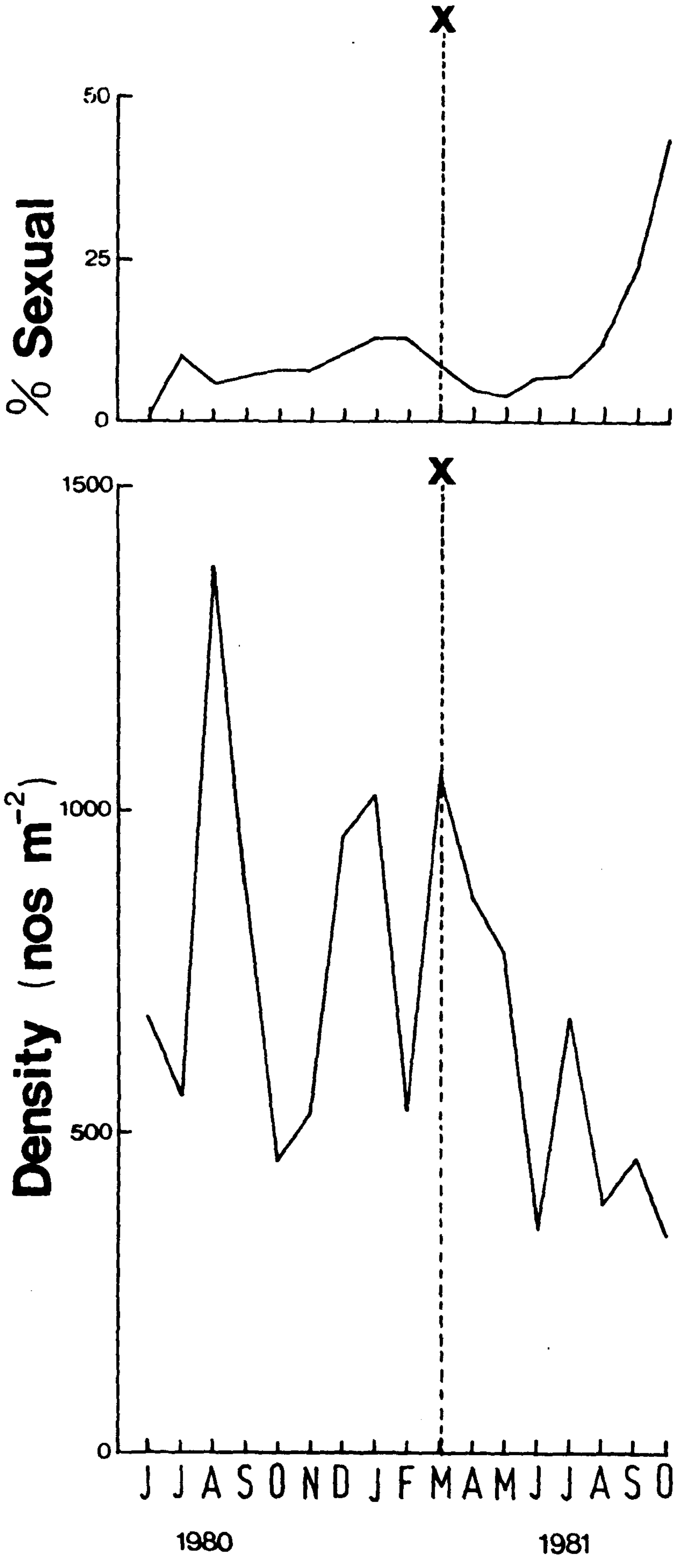
## FIGURE 37

Level of sexual reproduction (estimated as in Fig.30) in monthly samples at station 7 before (June 1980 to February 1981) and during (March 1981 to October 1981) the experimental period.

X denotes the start of the experimental period

## FIGURE 38

Population density at station 7 before (June 1980 to February 1981) and during (March 1981 to October 1981) the experimental period


X
50
25
0
% Sexual
X
1500
1000
500
0
Density (nos m$^{-2}$)
J J A S O N D J F M A M J J A S O
1980
1981

hypothesis. Such an experiment was carried out, and the methods involved and results obtained are described below.

The station chosen to carry out this manipulation was station 7 on the upstream area. Here it was evident that triclads occurred at high density, and the level of sexual reproduction was of a lower order than exhibited in the downstream population. The physically isolated nature of this station, and the fact that it enclosed only a small area of stream bed made it an ideal location for a manipulation experiment, since interference with the experimental conditions resulting from immigration of triclads from outside the study area was unlikely to occur.

The density manipulation was carried out by removing approximately 100 animals per month from the experimental area, and simultaneously monitoring the relative abundance of sexual and asexual individuals in the population, the density and the population size structure. It was originally planned to run the experiment for one year starting in March 1981 and completing in February 1982. Unfortunately, after 9 months, the experiment had to be completed prematurely when a landslide destroyed a large part of the study area.

The results of these manipulation experiments are presented in Figures 37 and 38. From these, it is evident that although there was apparently little change in the total size distribution, given in Fig. 28 (includes a separate presentation for station 7 of data collected before and during the experimental period), the density of the triclad population did decrease over the experimental period (see Fig. 38). Fig. 37 shows that the level of sexual reproduction, after an initial 'lag', increased from an initial level of 4% to a level of 44%, comparable with that exhibited by the downstream population. This remarkable increase in the level of sexual reproduction as a result of decreased triclad density occurred almost exponentially, and showed no evidence of 'slowing down' at the point when sampling was abandoned, following the landslide.

This series of observations is strongly supportive of the hypothesis described earlier. It seems likely, therefore, that the high levels of triclad density occurring at this station, and similarly at station 6, had resulted in correspondingly high levels of intraspecific competition between individuals in the population, high enough to apparently inhibit sexual reproduction. The experimental decrease in density caused by removal of individuals presumably reduced the intensity of intraspecific competition, and hence by effectively increasing net resource availability per triclad, caused a corresponding increase in the level of sexual reproduction within the population.

In order to test this hypothesis further, and in particular to examine more closely the particular environmental conditions which favour the occurrence of asexual reproduction in this species, laboratory studies examining the energy-partitioning strategies of this species under a variety of temperatures and ration levels, together with an examination of the effects of 'crowding' on sexual individuals (which could be carried out in the field or in the laboratory) would prove useful, and indeed were among the primary aims of this project when it was started. In order to carry out laboratory experiments on this species, however, the problems of lethal parasitic infections in laboratory must first be overcome, and the indications from this study, and others (Wright 1968; Lock 1972a) are that this could prove a major obstacle.

It should also be noted that this hypothesis does not attempt to explain the effects of cytogenetic factors on the occurrence of sexual and asexual reproduction in this species. Dahm (1958) has commented that, in this species, obligate asexual reproduction seems to be correlated with karyotype, but further work on this subject is required in order to confirm his observations. The link between karyotype and mode of reproduction has been clearly demonstrated in other triclad species, however, notably the Dugesiidae: Bromley (1977), for example, has shown that in _Dugesia biblica_, sexual reproduction is associated with diploidy, and asexual reproduction with triploidy.

Also, the work of Benazzi (1974) on _D.mediterranea_ has indicated that obligate asexuality may be genetically controlled by a gene-activated mechanism which inhibits the formation of germ cells, and there is some evidence to suggest that this 'switch' is under environmental control. Clearly, if such a mechanism occurs in _C.alpina_, an elaboration of the environmental conditions which control its activation could prove invaluable in understanding the relationship between environment and reproduction in this species.

# CHAPTER FOUR

# DISCUSSION

In the introductory chapter, the failure of the models produced in theoretical evolutionary studies (e.g. Maynard Smith 1978) to explain the possible short-term evolutionary advantages of sexual reproduction over asexual reproduction was attributed to the poorly defined natures of sexual and asexual reproduction. It has been customary in these studies to equate the process of sexual reproduction with the occurrence of meiosis, and hence parthenogenesis is considered as a form of asexual (their definition) reproduction. While there is nothing fundamentally wrong with this definition as it stands, in all aspects other than the absence of meiosis, parthenogenesis is similar to sexual reproduction, and hence it could be argued that it is more logical to class parthenogenesis with sexual reproduction than with fission or any of the other forms of asexual reproduction. I have argued that the process of gamete production, rather than the process of meiosis should be used as the primary criterion in distinguishing sexual reproduction, thus classifying parthenogenesis (both meiotic and ameiotic) as sexual reproduction, since it involves the production of gametes. I believe that this definition makes more biological sense, since a definition based on meiosis necessarily groups parthenogenesis and non-gametic forms of reproduction together. This clearly implies that parthogenesis has more in common with, e.g. fission, than with sexual reproduction, which is certainly true in that neither method involves meiosis. However, this classification fails to embrace fundamental biological differences between parthenogenesis (which involves the production of gametes by a recognisable 'reproductive system') and fission (which involves reproduction by somatic growth). Indeed, in all other processes involved in reproduction, parthenogenesis clearly has a greater affinity with sexual reproduction (for reasons described in Chapter 1) than with asexual reproduction (my definition). Also, it should be stressed that in parthenogenesis, meiosis is suppressed, whereas in asexual reproduction (my definition) meiosis is entirely redundant.

In the majority of studies considering the relative merits of sexual and asexual reproduction, the emphasis has been placed firmly on the relative genetic consequences of both types of reproduction, almost to the exclusion of other factors. In a number of recent studies, notably those of Calow et al. (1979) and Beveridge (1981), however, attempts have been made to discover the relative energetic costs of sexual and asexual reproduction, concentrating mainly on the processes of fission and cocoon production in freshwater triclads. In these studies, it has been demonstrated that the relative energetic efficiencies of fission and cocoon production vary. Cocoon production is more efficient at converting input resources into 'reproductive energy' (in terms of gamete production) whereas fission is more efficient in converting input resources into offspring (i.e. fission products). This has led to the prediction that fission should be favoured in trophically poor habitats (i.e. under situations of low resource availability), and cocoon production in habitats which are relatively less trophically poor (i.e. in situations where resource availability is <u>not always limiting</u> throughout the year). This prediction is supported by the fact that in the British Isles, asexually reproducing triclads are in general limited to lotic systems, which are considered to be of a lower trophic status than lentic systems (Reynoldson 1961b), although it should be emphasised that the relative trophic conditions in these habitats are based on personal judgement rather than on experimental evidence. Recently, Beveridge (1982) has extended these observations, noting that in triclads throughout the world, asexual reproduction is apparently favoured in streams, temporary habitats and "biotically unsaturated freshwater habitats", whereas sexual reproduction is favoured in situations where resource availability is only limiting for part of the year, if at all. The evidence presented in this study supports the latter observation concerning the occurrence of sexuality, but has shown that it is dangerous to generalise about the effects of the 'trophic status' of a freshwater habitat per se on the occurrence of specific reproductive patterns in freshwater triclads. To do so implies that it is the absolute availability of resources within a habitat which influences the relative occurrence of sexual and asexual reproduction within a population. In this study, it has been shown that in two adjacent habitats of similar 'trophic status', two populations of the same species exhibited radically different levels of sexual reproduction. The relationship demonstrated between population density and the level of sexual reproduction within these two populations has stressed the importance of considering the effects of factors within a population on its pattern of reproduction, in addition to the effects of variability in its habitat. Calow and Sibly (1982) use the term "growing conditions" to encompass the range of factors which influence resource-partitioning (and hence reproduction) in an organism throughout its life cycle, and this seems more suitable than the term 'trophic status', since it also includes the effects of factors within the population being considered. Their studies have recently extended the results for triclads, mentioned above, to produce theoretical models for invertebrates and protozoans. These models predict that asexual reproduction is favoured in poor "growing conditions" and sexual reproduction is promoted in good "growing conditions", and comment that in asexual reproduction, multiple fission should be favoured increasingly over binary fission as "growing conditions" improve. Interestingly, the point is also made that the general restriction of asexual reproduction (my definition) in the Animal Kingdom to the lower Metazoa is due to the fact that it is associated with the capacity of individuals to regenerate. In the higher Metazoa, regenerative capacity has, to a large extent, been sacrificed in a trade-off with increased tissue differentiation and specialisation. Beveridge (1982) comments that such a trade-off may have occurred within the Tricladida, suggesting that the lack of any asexually reproducing species in the Dendrocoelidae relates to the fact that this family generally possesses poor powers of regeneration. There seems strong evidence, therefore, to suggest that the environmental forces which select for efficient use of input resources, in terms of their conversion into reproductive output, in order to maximise fitness, may be of equal, if not greater, importance in deciding whether an animal reproduces sexually or asexually, than the selection of reproductive mechanisms purely on their relative ability to generate genetic diversity. In this present study, measurements of the relative levels of genetic variability existing in the populations at the upstream and downstream areas would have proved valuable in considering this possibility. Although a pilot study on the relative levels of enzyme variability between the two populations was carried out, the interpretation of these results proved difficult, and any conclusions drawn dubious, and for this reason, they are not presented here. Recent work on the genetic variability existing within strictly asexual populations of some species of freshwater triclad, i.e. the American species _Polycelis coronata_ (Nixon and Taylor 1977), and the British species _Polycelis felina_ (Beveridge, pers.comm.), has shown that genetic 'stasis' is not the inevitable fate of such groups. It should be stressed, however, that the genetic and energetic consequences of reproduction are necessarily inter-related, and that their relative importance may vary in different situations.

Having mentioned in the introductory chapter that the question of the long-term advantages of sexual reproduction over asexual reproduction had been answered convincingly by Williams (1975) and Maynard Smith (1978), it is now necessary to say that their approach considered only a comparison between sexual reproduction and parthenogenesis. I believe that the problem of the advantages of gametic reproduction over non-gametic reproduction (my definitions of sexual and asexual reproduction - see Table 1) have not yet been properly addressed. Although it is likely that the long-term advantages of sex over parthenogenesis (considered in terms of the ability to generate genetic diversity) may well apply similarly to a comparison of gametic and non-gametic forms of reproduction, this requires confirmation. However, the question of the short-term advantages of gametic reproduction over non-gametic reproduction may prove more tractable than the question Williams (1975) and Maynard Smith (1978) posed concerning the short-term advantages of sexual reproduction over parthenogenesis. Although answering the former question must take factors which select for genetic diversity into account, the evidence presented here strongly emphasises the need to obtain not only information on relative genetic variability within gametic and non-gametic populations, but also to identify the importance of genetic factors in relation to forces which select for greater energetic efficiency. In the short-term (i.e. from generation to generation), these latter forces may prove of major importance in determining the nature of reproduction within such populations.

Clearly, Williams' "crisis" mentioned in Chapter 1 is still with us, at least in terms of a comparison between sex and parthenogenesis. The re-definition of the meanings of 'sexual' and 'asexual' given here have done nothing to solve this "crisis", and indeed have undoubtedly compounded the problem, by introducing a further term for comparison (i.e. non-gametic reproduction). This was necessary, however, in order to emphasise that the paucity of work on the evolutionary ecology of 'non-gametic' populations (mentioned in Chapter 1) is a situation which urgently needs to be rectified.

# APPENDIX ONE

CALCULATION OF DENSITY ESTIMATES - a worked example

(see Section 3B (iii))

Calculation of Density Estimates: A worked example.

Giving hypothetical data (in this case for station 6 – see Chapter 3B(iii)), an estimate of density can be calculated as follows:

| Stone size categories | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| 'counts' (triclads/stone) | 1 | 0 | 3 | 4 |
| | 0 | 2 | 0 | 0 |
| | 1 | 6 | 4 | 11 |
| | 2 | 1 | 0 | 14 |
| | 0 | 0 | 0 | 0 |
| | 1 | 6 | 2 | 9 |
| | 3 | 0 | 0 | 0 |
| | 0 | 1 | 3 | 1 |
| | 0 | 0 | 6 | 23 |
| | 0 | 1 | 14 | 71 |
| $\Sigma x$ | 8 | 17 | 32 | 133 |
| $\bar{x}$ | 0.8 | 1.7 | 3.2 | 13.3 |

Given that the weighting factors for each mean value are as shown in Table 23 (see Chapter 3B(iii)), i.e. $y_1$ = 66.5; $y_2$ = 40.5; $y_3$ = 14.4; $y_4$ = 7.5, then the density estimate is calculated as:

$$\text{DENSITY (NOS.m}^{-2}) = (\bar{x}_1 y_1 + \bar{x}_2 y_2 + \bar{x}_3 y_3 + \bar{x}_4 y_4)$$

$$= (0.8 \times 66.5) + (1.7 \times 40.5) + (3.2 \times 14.4) + (13.3 \times 7.5)$$

$$= 53.20 + 68.85 + 46.08 + 99.75$$

$$= 276.88$$

i.e. calculated population density = $\underline{268 \text{ triclads.m}^{-2}}$

95% confidence limits for this estimate are calculated as :

$$t(p=0.05, N \text{ d.f.}) \times s \quad (s = \text{standard error})$$

where

$$s = \sqrt{V(\bar{x}_1 y_1 \; + \bar{x}_2 y_2 \; + \bar{x}_3 y_3 \; + \bar{x}_4 y_4 \;)}$$

in this case,

$$s = \sqrt{4405.51}$$

$$= \; 66.4$$

and 95% C.L. $= \; 2.02 \times 66.4$

$$= \; 134$$

the final density estimate is therefore

268 ± 134 triclads.$m^{-2}$

# APPENDIX TWO

Densities (± 95% C.L.) calculated from data collected over the period March 1980 to February 1982 according to the methods described in Chapter 3B(iii) - see text for details.

# STATION 1

| 1980 | | 1981 | |
|---|---|---|---|
| MAR | 30 ± 8.3 | MAR | 401 ± 53.2 |
| | NO DATA | | 153 ± 29.0 |
| APR | 147 ± 33.8 | APR | 264 ± 50.7 |
| | 121 ± 22.6 | | 60 ± 17.5 |
| MAY | 402 ± 78.1 | MAY | 364 ± 30.2 |
| | 189 ± 38.7 | | 128 ± 12.0 |
| JUN | 225 ± 42.4 | JUN | 243 ± 21.9 |
| | 246 ± 50.1 | | NO DATA |
| JUL | 287 ± 54.1 | JUL | 260 ± 20.6 |
| | 221 ± 47.4 | | 251 ± 23.7 |
| AUG | NO DATA | | 325 ± 28.8 |
| | 79 ± 13.8 | AUG | 161 ± 20.2 |
| SEP | NO DATA | | 108 ± 10.9 |
| | 31 ± 8.5 | SEP | 163 ± 19.7 |
| OCT | 72 ± 20.0 | | NO DATA |
| | 156 ± 27.4 | OCT | 66 ± 13.6 |
| NOV | 114 ± 30.0 | | NO DATA |
| | 59 ± 24.4 | NOV | 64 ± 7.4 |
| DEC | 15 ± 4.8 | | 145 ± 19.8 |
| | 87 ± 25.9 | DEC | NO DATA |
| | NO DATA | | 144 ± 37.6 |
| 1981 | | 1982 | |
| JAN | NO DATA | JAN | 71 ± 6.4 |
| | 121 ± 25.7 | | NO DATA |
| FEB | 35 ± 8.8 | FEB | 70 ± 10.3 |
| | 329 ± 65.9 | | 44 ± 9.1 |

# STATION 3

| 1980 | | 1981 | |
|---|---|---|---|
| MAR | 214 ± 46.9 | MAR | 608 ± 108.8 |
| | NO DATA | | 384 ± 49.3 |
| APR | 361 ± 104.0 | APR | 409 ± 66.2 |
| | 472 ± 66.3 | | 342 ± 45.8 |
| MAY | 716 ± 138.6 | MAY | 414 ± 39.8 |
| | 633 ± 103.7 | | 513 ± 46.8 |
| JUN | 158 ± 39.7 | JUN | 480 ± 55.0 |
| | 218 ± 54.6 | | NO DATA |
| JUL | 244 ± 35.0 | JUL | 181 ± 14.4 |
| | 137 ± 16.1 | | 299 ± 39.9 |
| AUG | NO DATA | | 176 ± 16.7 |
| | 219 ± 39.8 | AUG | 206 ± 17.5 |
| SEP | NO DATA | | 148 ± 14.0 |
| | 47 ± 10.6 | SEP | 315 ± 24.0 |
| OCT | 151 ± 26.0 | | NO DATA |
| | 411 ± 44.6 | OCT | 73 ± 7.1 |
| NOV | 568 ± 123.4 | | NO DATA |
| | 275 ± 49.4 | NOV | 352 ± 33.0 |
| DEC | 214 ± 33.4 | | 232 ± 19.1 |
| | 120 ± 15.0 | DEC | NO DATA |
| | NO DATA | | 275 ± 32.0 |
| 1981 | | 1982 | |
| JAN | NO DATA | JAN | 269 ± 25.0 |
| | 276 ± 51.6 | | NO DATA |
| FEB | 405 ± 56.3 | FEB | 353 ± 29.0 |
| | 567 ± 106.7 | | 727 ± 52.6 |

# STATION 4

| 1980 | | 1981 | |
|---|---|---|---|
| MAR | 160 ± 70.1 | MAR | 135 ± 37.8 |
| | NO DATA | | 112 ± 34.5 |
| APR | 447 ± 142.0 | APR | 503 ± 68.4 |
| | 258 ± 39.7 | | 270 ± 23.9 |
| MAY | 535 ± 114.4 | MAY | 250 ± 33.5 |
| | 87 ± 22.4 | | 431 ± 57.5 |
| JUN | 120 ± 21.6 | JUN | 370 ± 46.4 |
| | 471 ± 201.9 | | NO DATA |
| JUL | 181 ± 38.3 | JUL | 671 ± 104.4 |
| | 168 ± 24.4 | | 197 ± 35.7 |
| AUG | NO DATA | | 430 ± 54.9 |
| | 233 ± 59.0 | AUG | 484 ± 62.3 |
| SEP | NO DATA | | 115 ± 12.5 |
| | 50 ± 17.1 | SEP | 149 ± 15.8 |
| OCT | 94 ± 33.9 | | NO DATA |
| | 332 ± 99.3 | OCT | 49 ± 8.0 |
| NOV | 396 ± 67.1 | | NO DATA |
| | 101 ± 28.0 | NOV | 128 ± 17.6 |
| DEC | 240 ± 53.4 | | 241 ± 26.6 |
| | 355 ± 80.8 | DEC | NO DATA |
| | NO DATA | | 230 ± 30.5 |
| 1981 | | 1982 | |
| JAN | NO DATA | JAN | 242 ± 36.9 |
| | 53 ± 13.8 | | NO DATA |
| FEB | 124 ± 56.5 | FEB | 166 ± 20.0 |
| | 154 ± 106.7 | | 311 ± 32.6 |

# STATION 6

| 1980 | | 1981 | |
|---|---|---|---|
| MAR | 445 ± 82.5 | MAR | 375 ± 37.8 |
| | NO DATA | | 399 ± 34.5 |
| APR | 526 ± 75.8 | APR | 566 ± 68.4 |
| | 624 ± 154.3 | | 622 ± 23.9 |
| MAY | 581 ± 73.7 | MAY | 618 ± 33.5 |
| | 454 ± 55.7 | | 379 ± 57.5 |
| JUN | 597 ± 89.7 | JUN | 468 ± 46.4 |
| | 455 ± 60.5 | | NO DATA |
| JUL | 606 ± 111.8 | JUL | 564 ± 104.4 |
| | 454 ± 67.6 | | 567 ± 35.7 |
| AUG | NO DATA | | 454 ± 54.9 |
| | 568 ± 61.5 | AUG | 697 ± 62.3 |
| SEP | NO DATA | | 405 ± 12.5 |
| | 511 ± 54.8 | SEP | 579 ± 15.8 |
| OCT | 669 ± 83.5 | | NO DATA |
| | 1040 ± 148.5 | OCT | 467 ± 8.0 |
| NOV | 608 ± 97.1 | | NO DATA |
| | 489 ± 49.8 | NOV | 573 ± 17.6 |
| DEC | 600 ± 99.9 | | 441 ± 26.6 |
| | 424 ± 64.1 | DEC | NO DATA |
| | NO DATA | | 443 ± 30.5 |
| 1981 | | 1982 | |
| JAN | NO DATA | JAN | 780 ± 37.0 |
| | 874 ± 144.7 | | NO DATA |
| FEB | 382 ± 45.3 | FEB | 452 ± 20.0 |
| | 727 ± 79.2 | | 589 ± 32.6 |

# STATION 7

| 1980 | | 1981 | |
|---|---|---|---|
| MAR | NO DATA | MAR | 1516 ± 258.9 |
| | NO DATA | | 595 ± 92.4 |
| APR | NO DATA | APR | 966 ± 150.3 |
| | NO DATA | | 818 ± 88.6 |
| MAY | NO DATA | MAY | 668 ± 99.0 |
| | NO DATA | | 889 ± 126.4 |
| JUN | NO DATA | JUN | 349 ± 39.0 |
| | 683 ± 150.7 | | NO DATA |
| JUL | 345 ± 60.5 | JUL | 689 ± 107.2 |
| | 766 ± 105.2 | | 717 ± 87.4 |
| AUG | NO DATA | | 632 ± 92.8 |
| | 1377 ± 220.2 | AUG | 433 ± 42.1 |
| SEP | NO DATA | | 346 ± 60.4 |
| | 881 ± 154.6 | SEP | 459 ± 50.8 |
| OCT | 395 ± 47.5 | | NO DATA |
| | 506 ± 76.5 | OCT | 340 ± 40.4 |
| NOV | 521 ± 79.5 | | NO DATA |
| | 538 ± 50.5 | NOV | 253 ± 40.4 |
| DEC | 1402 ± 182.1 | | NO DATA |
| | 519 ± 84.4 | DEC | NO DATA |
| | NO DATA | | NO DATA |
| 1981 | | 1982 | |
| JAN | NO DATA | JAN | NO DATA |
| | 1022 ± 143.2 | | NO DATA |
| FEB | 465 ± 82.0 | FEB | NO DATA |
| | 604 ± 138.7 | | NO DATA |

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