The Role of Interspecific Competition in the Distribution of two Stream Dwelling Triclads, Crenobia alpina (Dana) and Polycelis felina (Dalyell), in North Wales

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THE ROLE OF INTERSPECIFIC COMPETITION IN THE DISTRIBUTION OF TWO STREAM DWELLING TRICLADS, *CRENOBIA ALPINA* (DANA) AND *POLYCELIS FELINA* (DALYELL), IN NORTH WALES

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INTRODUCTION

Wright (1968, 1972, 1974) investigated the distribution of *Crenobia alpina* (Dana) and *Polycelis felina* (Dalyell) in North Wales and concluded that temperature, water chemistry, predation and parasitism did not appear to be important parameters in this area. Two factors he identified being involved were the gradient of the stream and interspecific competition. The role of gradient, its associated water flow and substratum have been examined by Lock (1972a, 1975) and it was concluded that the restriction of *P. felina* in shallow gradients was a behavioural response whilst the restriction of *Crenobia alpina* in steeper gradients may be due to the competitive superiority of *Polycelis felina* in shallow gradient habitats. This hypothesis is examined here.

It was first suggested by Voigt (1892, 1904) that competition influenced the distribution of *Crenobia alpina* and *Polycelis felina*. However, the later work of Beauchamp & Ullyot (1932) is better known and is often quoted as an example of 'interspecific competition'. Criticism of this paper can be found in Andrewartha & Birch (1954), Miller (1967) and Reynoldson & Bellamy (1970). Wright (1968) did not consider that interspecific competition was taking place in the larger streams (width 2–5 m); however, in the small springfed streams of shallow gradient (<27%) where temperature never became limiting, *P. felina* appeared to displace *Crenobia alpina*. He also produced limited evidence from feeding experiments and gut squashes that they both fed on the same prey organisms.

Reynoldson & Bellamy (1970) identified the following five criteria as being appropriate evidence of interspecific competition. It is within this scheme that the evidence for interspecific competition between the two triclads has been examined.

(1) The comparative distribution and/or relative abundance of the two potentially competing species should be amenable to explanation based on competition.

(2) It is necessary to show that the competing species are utilizing a common resource which may provide the basis of competition.

(3) There should be evidence from the performance of the particular species population in the field that intraspecific competition is occurring.

(4) Both the resource which is being competed for and the population should be manipulated separately in the field with predictable results based upon the hypothesis that competition is occurring.

(5) Events following the introduction or removal (or reduction) of a competing species should be consistent with the competition hypothesis.

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METHODS

Triclads were sampled throughout this study by timed collections (Reynoldson 1966) and were collected with a paintbrush from the undersides of stones for a standard period of 10 min. The triclads were identified and counted in the laboratory, and were then returned to their corresponding station in the stream, usually within two to three days. Although this method produces comparative data only for samples from the same station, it is probably reasonable to draw comparison between stations of similar bottom type. The more usual methods of sampling streams quantitatively (e.g. Surber-type sampler) were unsuitable because of the delicate nature of triclads. It was not possible to use slates or trays of substratum (Reynoldson & Young 1963) because these methods do not lend themselves to a regular sampling programme in a stream.

Evidence of interspecific .competition was looked for in streams or sections of small spring-fed streams with gradients and temperature regimes suitable for both species. Such streams were found in the Anafon Valley, Anafon stream A and Anafon stream B, and some of the head streams feeding the Nant Heilyn stream (Wright 1974).

The results are presented within the scheme suggested by Reynoldson & Bellamy (1970) as outlined in the introduction. More detailed methods are presented in the appropriate sections.

Comparative distribution and abundance

Evidence in this category is based upon the small spring-fed streams of the Anafon valley and from the spring head system of Nant Heilyn. Although *Crenobia alpina* occurred in the Anafon streams throughout their length, it was only dominant on the steep-gradient. and was the only species of triclad at several such stations. However, on the shallow-gradient regions of the stream, where *Polycelis felina* occurred, *Crenobia alpina* formed on average only 20% of the total *Polycelis felina* + *Crenobia alpina*. At the spring-head system of the Nant Heilyn, Wright (1968) had recorded *C. alpina* from nine out of the fourteen sources. Of these nine, two also contained populations of *Polycelis felina* but he gave no indication of the proportion. During our initial survey in the winter of 1969–70 we had been unable to find any *P. felina* in either of these two sources yet during a collection of *Crenobia alpina* for laboratory work in September of 1970, a large population of *Polycelis felina* was found in one of the other streams previously containing only *Crenobia alpina*. The ratio of *Polycelis felina*/*Crenobia alpina* at the latter source was 75% to 25% and it remained at around this level for fifteen months at which point there was a sudden reversal of the proportions. This sudden change was unlikely to have been the result of competition but was probably due to some catastrophic event. These events will be considered in greater detail later in the paper.

Common resource

Reynoldson has presented a considerable amount of evidence (Reynoldson 1966; Reynoldson & Davis 1970; Reynoldson & Bellamy 1970) supporting the hypothesis that interspecific competition for food determines the distribution of the four common species of lake-dwelling triclads, *Polycelis tenuis* (Ijima), *P. nigra* (Müll.), *Dugesia polychroa* (Schmidt) and *Dendrocoelum lacteum* (Müll.). It therefore seemed possible that food might also form the basis for competitive interactions in *Crenobia alpina* and

Polycelis felina. Although Wright (1968) had produced limited evidence for this, the obvious approach was to use the 'Precipitin-test' (Young, Morris & Reynoldson 1964; Reynoldson & Davies 1970; Sefton 1969; Pickavance 1971; Boddington & Mettrick 1974).

Methods

As there are two recent papers on the methodology and application of the precipitin test in feeding studies (Davies 1969; Pickavance 1970), the procedure will be only

Table 1. *Cross-reactions of the five antisera with other antigens*

	Anti-Ephemeropteran	Anti-Plecopteran	Anti-Trichopteran	Anti-*Gammarus*	Anti-Oligochaeta
Crenobia alpina	−	−	−	−	−
Polycelis felina	−	−	−	−	−
Phagocata vitta (Dugès)	−	−	−	−	−
Lumbricidae sp.	−	−	−	−	−
Lumbriculus variegatus (Müll.)	−	−	−	−	−
Lumbriculus sp.	−	−	−	−	*
Tubificidae	−	−	−	−	−
Stylodrilus sp.	−	−	−	−	*
Allolobophora longa (Ude)	−	−	−	−	+
Gammarus pulex (Linn.)	−	−	−	+	−
Baetis rhodani (Pict.)	+	−	−	−	−
B. muticus (Linn.)	+	−	−	−	−
Rhithrogena semicolorata (Curt.)	+	−	−	−	−
Ecdyonurus venosus (Fab.)	+	−	−	−	−
Helodes sp.	−	−	*	−	−
Nemoura sp.	−	+	−	−	−
Leuctra sp.	−	+	−	−	−
Isoperla grammatica (Poda)	−	+	−	−	−
Dinocras cephalotes (Curt.)	−	+	−	−	−
Diura bicaudata (Linn.)	−	+	−	−	−
Agapetus fuscipes (Curt.)	−	−	+	−	−
Psychomyiidae sp.	−	−	+	−	−
Philopotamidae sp.	−	−	+	−	−
Hydropsychidae sp.	−	−	+	−	−
Plectrocnemia sp.	−	−	+	−	−
Limnephilidae sp.	−	−	+	−	−
Tipulidae (sp. 1)	−	−	−	−	−
Tipulidae (sp. 2)	−	−	−	−	−
Chironomidae (sp. 1)	−	−	−	−	−
Chironomidae (sp. 2)	−	−	−	−	−
Simuliidae sp.	−	−	−	−	−
Ancylus fluviatilis (Müll.)	−	−	−	−	−
Limnaea truncatula (Müll.)	−	−	−	−	−
Pisidium sp.	−	−	−	−	−

* Weak reaction.

outlined except where modifications have been made. The test first involves injecting a mammal (usually a rabbit) with a protein solution of the suspected food organism (antigen), to which antibodies are then produced in the blood serum (antiserum). Potential predators collected in the field either have their gut removed and a macerate of this tested or as in the case of triclads, the whole animal is macerated and this is then used in the precipitin test. The particular precipitin method adopted was that first described by Ouchterlony (1948), one of the three methods commonly used (see Davies 1969). The antigen and antibody were allowed to diffuse out from adjacent wells cut in a 2-mm layer of 0·65% Ionagar No. 2 in 0·85% saline with 1% sodium azide. A positive

reaction was indicated by a white precipitin band occurring transversely between the two wells. A modification of the usual methods of storage and subsequent testing of the triclads was made. Each one was placed on filter paper rather than squashed and then stored at −20° C. Test animals were usually in the deep-freeze within 2 h of collection. After storage for a few weeks at this temperature the triclads became effectively freeze-dried and on removal from storage they could be dislodged easily from the filter-paper with the aid of a chisel-shaped spatula. The triclads were then placed into 50×5 mm tubes containing 0·03 ml of 0·85 saline and allowed to stand for 30 min–1 h. They were then brought into suspension by using a vibratory mixer (Fisons-Whirlimixer). The highly concentrated triclad extract was introduced into a central well and was tested simultaneously with several antisera placed in wells around it. The decrease in sensitivity of the Ouchterlony method (Davies 1969) over that of the modified Oakley-Fulthorpe method (Morris 1964) was offset by these two factors.

Antisera were produced against each of the major components of the stream fauna: *Gammarus pulex* (Linn.), Oligochaeta, Ephemeroptera, Plecoptera and Trichoptera. Ephemeroptera were mainly *Rhithrogena semicolorata* (Curt.), Plecoptera were *Dinocras cephalotes* (Curt.) and *Isoperla grammatica* (Poda), Trichoptera were mainly *Agapetus fuscipes* (Curt.). The Oligochaeta antisera were produced by injecting rabbits with the earthworm *Allolobophora longa* (Ude). Each of the antisera was tested against the other major stream inhabitants to check for the extent of cross-reactions. Table 1 shows that in relation to the potential prey of triclads available in the stream habitat, the anti-Ephemeropteran serum was specific to the Ephemeroptera, the anti-Plecopteran specific to the Plecoptera, the anti-Trichopteran specific to the Trichoptera with a weak cross-reaction with a helodid beetle, and anti-*Gammarus* specific to *Gammarus pulex*. The anti-oligochaete serum reacted strongly with *Allolobophora longa* but only produced very weak reactions with *Lumbriculus sp.* and *Stylodrilus sp.*, two species likely to be found in the streams. In the testing of the triclads from the field only the first four antisera were finally used as the anti-oligochaete serum was too weak to be useful.

Results and discussion

Because of possible specific differences in rates of digestion and differing sensitivities of the antisera, it is necessary to know how long after feeding the various antigens can be detected in each triclad species. For this purpose triclads of both species were allowed to feed to repletion and then tested against the antisera over a range of time intervals. During the time intervals the triclads were held at 10° C because Davies (1967) had shown that the detection period varied with temperature. Since the temperature of the stations varied from only 8–11° C over the year, a single detection period at 10° C was considered sufficient. The results of the detection period study for *Crenobia alpina* and *Polycelis felina* are respectively twelve and ten days for anti-*Gammarus*, six and four and a half days for anti-Ephemeroptera, eleven and twelve days for anti-Plecoptera and finally ten and eight days for anti-Trichoptera.

The food of these triclads was studied by taking specimens from Nant Heilyn spring streams 3 and 5 (Wright 1968) which were only 20 m apart; spring 5 had only *Crenobia alpina* and spring 3 had both species. The populations are referred to respectively as Control-*C. alpina*, Mixed-*C. alpina* and Mixed-*Polycelis felina*. Samples were taken at three to four-month intervals and extended over a period of a year. The triclads were stored at −20° C as indicated earlier in this section and each triclad tested with the four antisera.

The data on positive reactions are presented below. Of the Control-*Crenobia alpina*, 166 were tested, giving 183 positive reactions which represented 110% of those tested. Of the Mixed-*C. alpina*, 137 were tested, giving eighty positive reactions representing 58% of those tested, and finally, of the Mixed-*Polycelis felina*, 169 were tested, giving 120 positive reactions which represented 71% of those tested. A total of 472 triclads were tested which yielded 383 positive reactions.

Before comparing the food of the three populations, the data have first to be corrected for the detection period. The detection period of Trichoptera in *P. felina* was taken as unity and the others were calculated in relation to it (Table 2).

As the technique is a qualitative one, this poses a problem in the interpretation of the data. However, the assumption of Reynoldson & Davies (1970) is followed, where each positive is regarded as a single meal on the prey identified. Shortcomings of this assumption are that larger triclads might take larger meals with longer detection periods and that a single positive may represent more than one meal upon that prey. However, as Reynoldson & Davies (1970) point out, a double meal will increase the amount of that food in the gut and consequently lengthen the detection period. The adjusted positive

Table 2. *Food of the three populations based upon adjusted positive immunological tests expressed as a percentage of total positive tests*

	Gammarus	Ephemeroptera	Plecoptera	Trichoptera	Total tested	Positive reactions
Control-*Crenobia alpina*	44	0	25	31	166	131
Mixed-*C. alpina*	8	0	38	54	137	60
Mixed-*Polycelis felina*	32	4	24	40	169	102

reactions for each of the food items in respect of the three triclad populations are presented in Table 2. Ephemeroptera were preyed upon to a negligible extent by all populations. With the exception of the Mixed-*Crenobia alpina* populations which fed to only a a limited extent upon *Gammarus*, the remainder of the positives for each population relating to *Gammarus*, Plecoptera and Trichoptera are of the same order.

In the ensuing section an examination will be made of the food-niches of the three populations to determine the extent of 'niche-overlap' between them. The 'food refuge' concept was introduced by Reynoldson (1966) and is defined as that food component for which the particular triclad species is competitively superior to other triclad species and therefore usually forms the largest component of its 'food niche'. Intraspecific competition for the 'food refuge' will be mainly responsible for population regulation (Reynoldson 1964). If two species have the same 'food refuge' then theoretically it would be expected that one or other would be eliminated (Hutchinson 1957; Hardin 1960). Reynoldson & Davies (1970) showed that in the lake-dwelling triclads the 'food refuge' formed 40–80% of the total 'food niche'. As the difference between corresponding pairs of animals is the relevant feature they did this for all pair combinations of the triclads examined.

This procedure could not be adopted here because of the absence of data for the oligochaete niche. Instead, the adjusted percentage positive reactions for each food category tested were compared directly between each triclad population (Table 2). Since Ephemeroptera were preyed upon to such a limited extent they will be excluded from the discussion of food niche overlap. The Trichoptera and Plecoptera were extensively preyed upon by both species, and to relatively similar degrees in the mixed situation.

It therefore seems reasonable to conclude that a 'food refuge' would not exist in either of those two prey groups. However, the feeding of *Crenobia alpina* upon *Gammarus* shows that in the control situation it formed 44% of the total positives but in the mixed situation it formed only 8%. This suggests that in the presence of *Polycelis felina, Crenobia alpina* was unable to secure its 'normal' compliment of *Gammarus*. It is also pertinent to draw attention to the earlier observation on the total percentage positive reactions for all antisera. *Crenobia alpina* occurring alone had 110% positives while in the mixed situation it had only 58% positives. This suggests that *C. alpina* was under competitive stress in the mixed situation with the reduction of positive reactions possibly due to the more successful feeding of *Polycelis felina* upon *Gammarus*.

Although considerable food overlap has been demonstrated with the antisera used, the possibility remains that not all the important prey of the triclads have been covered; an obvious gap is oligochaetes. Fortunately, Wright (1968) carried out gut-squashes on both species and found by examination of chaetae that they were feeding on essentially the same type of oligochaetes to a similar extent with *Crenobia alpina* taking slightly more of the Naididae. Of the triclads examined, about 30% had oligochaete remains in their gut. Thus with the antisera and the gut-squash analyses of Wright, it would appear that the major food groups have been covered.

Performance of field populations

Reynoldson & Bellamy (1970) were able to draw on three pieces of field evidence which indicated that intraspecific competition for food was strong. They argued that if species were co-existing and competing, then intraspecific competition must also be occurring and acting to regulate population numbers. (An outline of the population biology of sexually reproducing triclads can be found in Reynoldson (1966).)

Their evidence was: (i) shrinkage of adults when young appear in the population; (ii) low fecundity of adults in established populations compared with laboratory animals fed once weekly and with adults in a population considerably below the carrying capacity of the habitat (Reynoldson 1975); (iii) highest mortality in small individuals following recruitment.

Size/frequency data were collected for Control-*C. alpina*, Mixed-*C. alpina* and Mixed-*Polycelis felina* populations. However, little information could be extracted from them. This was due to an inability to differentiate young and 'shrunken' individuals and to determine the time of recruitment. The latter was a consequence of the cocoons being laid free and thus being almost impossible to find in the field.

Extensive attempts were made to rear both species in the laboratory to obtain fecundity estimates and to carry out competition experiments. However, this proved impossible as the populations inevitably succumbed to a fatal ciliate infection, probably *Tetrahymena pyriformis* (Ehrenberg) (Wright 1968) despite the use of prophylactics and quarantining.

Manipulation of the resource

Reynoldson & Bellamy (1970) suggested that in the manipulation of the resources it was insufficient to just increase the available food but that the population should be separately manipulated with results consistent with the hypothesis that competition was occurring. An increase in the food could cause a response from a population whether it was under competitive stress or not, as the same amount or more food might be obtained with less expenditure of energy. Taylor & Reynoldson (1962) found in two small populations living in restricted habitats that the addition of food in one and a reduction of the

pre-breeding population in the other markedly alleviated the symptoms of intraspecific competition as indicated by Criterion 3. These two approaches posed the considerable technical problem of restricting a portion of the stream population in some way. As Wright (1968) made extensive but unsuccessful attempts to do this, the possibility of manipulating unrestricted populations had to be considered. The continuous addition of food to a non-restricted area would be likely to attract more triclads into the area and therefore nullify the aims of the experiments. It was decided therefore to attempt to manipulate the population rather than the food. It was realized at the outset that immigration would be likely to occur but it was intended to conclude the experiment in a few months thereby reducing the impact of this factor.

The alleviation of symptoms of intraspecific competition was determined by measuring the levels of a food reserve lyo-glycogen (Jennings 1957) before and after the perturbation. Boddington & Mettrick (1971) showed that lyo-glycogen decreased exponentially with an increase in number of triclads in the population and that its negative regression coefficient on population biomass was significant. Such results were consistent with Reynoldson's (1966) hypothesis that triclad numbers are regulated by competition for food, since, as the population size increases, intraspecific competition for food results in a decrease in the lyo-glycogen food reserve. It was realized that this approach was a tentative one but it is reported because it would appear to have potential in analysing competitive interactions in the field where food is the focus of the competitive effort. However, it is possible that other parameters, e.g. the energy value of the triclads, might be found to be better indices.

Methods

Two populations of each species were selected, one to act as a control and one as the experimental population. The *Crenobia alpina* experimental population inhabited a steep-gradient section of Anafon B (42%) where *Polycelis felina* had not been found over a period of twelve months sampling. The control population was the Control-*Crenobia alpina* population of Nant Heilyn stream 5 used in the section on 'Common resource'. The *Polycelis felina* experimental population was in a section of a stream (8% gradient) near Foel Ganol (Nat. Grid ref. SH 680720). This contained around 1% *Crenobia alpina* which was considered unlikely to interfere with the experiment. The control occupied station 5 of Anafon A (gradient 12%) and also contained 1–2% *C. alpina*. It is necessary to point out that the controls employed in this experiment were not rigorous ones, their choice was dictated by force of circumstances. Triclads for lyo-glycogen analysis were placed into weighed tissue grinders and freeze-dried over a period of 15 h; after the drying they were immediately weighed.

The lyo-glycogen extraction was by Tricholoro Acetic Acid (T.C.A.) at 10° C for a period of 30 min. Initially 2 cm³ of T.C.A. were added to each homogenizer and the triclads ground up, then further T.C.A. was added, the amount depending upon the weight of tissue present, allowing approximately 2 cm³ T.C.A. per milligram of tissue. After allowing the tubes to stand for the required period, the liquid was mixed once again and then the solid spun down. The resulting extract was stored at 2° C until testing; this was usually within two to three days. The method of estimation of lyo-glycogen was slightly modified from Trevelyan & Harrison (1952).

At the start of the experiment, 10-min collections of triclads were taken and analysed in the laboratory for lyo-glycogen. Excess animals from the control populations were returned to the field. The reduction of the population in the two experimental populations

Table 3. *Changes in numbers and lyo-glycogen levels of the control and reduced populations of* Crenobia alpina *and* Polycelis felina *over a two-month period*

| | Crenobia alpina | | | | | | Polycelis felina | | | | | |
| | Control | | | Reduced | | | Control | | | Reduced | | |
	Start	Month 1	Month 2	Start	Month 1	Month 2	Start	Month 1	Month 2	Start	Month 1	Month 2
Number/10 min	214	176	76	249	69	50	244	354	162	383	155	189
No. individual/sample	20	20	20	50	50	50	50	50	50	50	50	50
Lyo-glycogen µg/mg dry wt	76·9	73·5	83	58·5	87·3	71·1	99·1	56·3	105·8	65·0	113·1	112·4

was achieved by baiting with pieces of lumbricid worm; in this way 2000+*Polycelis felina* were removed and about 1000+ *Crenobia alpina*. Two subsequent 10-min samples were analysed from each of the populations at an interval of one month. The lyo-glycogen determinations were carried out on pooled samples of triclads which had been adjusted to the size-frequency distributions of the original samples. This minimized possible errors due to differences in the size structure of triclads.

Results and discussion

Baiting succeeded in reducing the *C. alpina* experimental population from 249/10 min to 69/10 min, and the *Polycelis felina* population from 383/10 min to 155/10 min (Table 3). However, because of population changes through unknown factors in the controls, the control data could no longer be used. Consequently changes in the experimental populations refer to the initial level only.
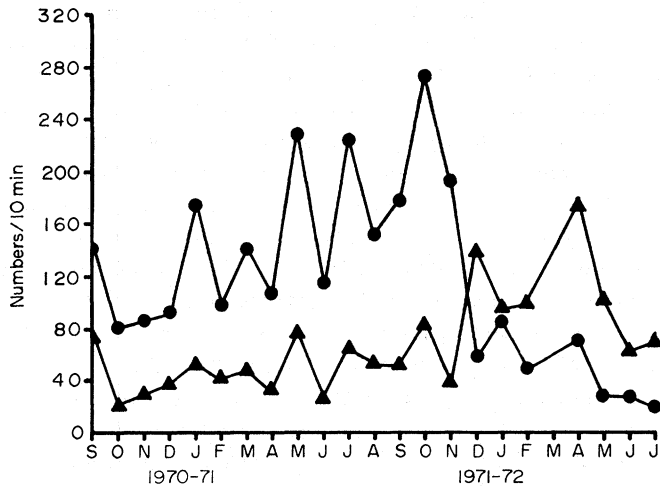

FIG. 1. Numbers per 10 min of the Mixed-*Crenobia alpina* (▲) and Mixed-*Polycelis felina* (●) over a period of twenty-two months.

Examination of the lyo-glycogen data (Table 3) for the *Crenobia alpina* experimental population shows a steep rise in the first month from an initial level of 59 μg/mg dry wt to 87 μg/mg dry wt and then a decline over the second month to 71 μg/mg dry wt. The corresponding data for *Polycelis felina* shows a sharp rise from 65 μg to 113 μg/mg dry wt, which remains at about that level for the second month.

The fact that the lyo-glycogen levels behaved as predicted based on the competition hypothesis supports this argument but the erratic behaviour of the controls detracts from it.

Manipulation of the species

An obvious place for manipulation of the species was in the Nant Heilyn spring system where, as described earlier (p. 582) *P. felina* had come to occupy a shallow-gradient spring stream previously containing only *Crenobia alpina*. The intention was to make an introduction of *Polycelis felina* into a stream containing only *Crenobia alpina* such that they formed a large percentage of the total triclad population, with the possibility that

they could then exert competitive pressure upon the *C. alpina* Two attempts were made to do this in a shallow-gradient spring (15%) containing only *C. alpina* but these were unsuccessful. It seems unlikely that this was due to a competitive interaction as the *Polycelis felina* disappeared too quickly (within three to four months) and was possibly due to the stream current/substratum complex being unsuitable.

Fortunately, a natural experiment of this sort presented itself while monitoring the Mixed *P. felina/Crenobia alpina* population of Nant Heilyn stream 3. Examination of the absolute numbers of *C. alpina* and *Polycelis felina* per 10 min (Fig. 1) for the first fifteen months of this period up to November 1971 showed that *P. felina* was the dominant triclad with a mean of 151/10 min (S.E. $\pm$ 16·0), the corresponding mean for *Crenobia alpina* being 48/10 min (S.E. $\pm$ 5·4). After November 1971 the mean for *Polycelis felina* dropped dramatically to 49/10 min (S.E. $\pm$ 9·3) for the remaining period of the study and *Crenotia alpina* increased to a mean level of 107/10 min (S.E. $\pm$ 14·9). On comparing each pair of means using a *t*-test for low numbers, where the variances are not assumed equal (Bailey 1959), they were found to be significantly different: $t = 3·68$ (7·6 d.f. $P < 0·01$) for *C. alpina* and $t = 5·45$ (19·8 d.f. $P < 0·01$) for *Polycelis felina*. The proportional changes are presented in Fig. 1. For the fifteen months prior to the *P. felina* 'crash' *Crenobia alpina* formed around 20% of the total population but after the 'crash' it assumed 70% of the total. This then seems evidence of the operation of interspecific competition, where the removal of a 'dominant' species allows an increase in the numbers of an 'inferior' species. It seems unrealistic to regard this event as being due to chance. Examination of the size-structure of *C. alpina* over this period did not suggest that recruitment was taking place via breeding (Lock 1972b). This leads one to suspect that immigration, possibly from underground reservoirs at the spring head (Wright 1968) was responsible for the increase in numbers. The sudden crash in numbers of *Polycelis felina*, prior to this event, may have been due to severe rains and consequent alteration in character of the stream from being rather slow and choked with macrophytic vegetation to a one which was rather swift and canalized. From the evidence presented earlier (Lock 1972a, 1975), *P. felina* is not tolerant of swift flowing conditions and the substratum/current complex may have been altered such that it became unsuitable for it. It is interesting to speculate as to the final outcome of this situation. If there was just a 'flushing out' of *P. felina* it might be expected that it would increase in numbers again at this station. This does not appear to be happening (Fig. 1) suggesting that a rather more permanent change has taken place.

CONCLUSION

Evidence from the comparative distribution and abundance of *Crenobia alpina* and *Polycelis felina* is consistent with the occurrence of competition yet cannot be conclusive on its own. It was also possible to present good evidence of a common resource as a basis of competition in that an examination of the major food items suggests that a food refuge is not present for either species. The use of size frequency data was not a suitable parameter to use as evidence of interspecific competition. Manipulation of the individual populations combined with monitoring the levels of a food reserve lyoglycogen provided tentative evidence of the alleviation of intraspecific competition. Finally, the results of a natural alteration of the species was observed; after a crash in the numbers of the dominant *P. felina* in a mixed situation, *Crenobia alpina* became the dominant triclad.

Although the evidence for some of the criteria is not strong, collectively it suggests that interspecific competition was occurring between these two triclads and could account for the absence of *C. alpina* in a majority of the shallow-gradient habitats.

Finally, it is necessary to consider the case of co-existence of *C. alpina* and *Polycelis felina* in the shallow-gradient regions of Anafon B and at the Nant Heilyn spring system where only *P. felina* would be expected in the light of this conclusion. Three possibilities are suggested which might account for such co-existence: (i) persistent immigration from upstream or from possible underground populations (Wright 1968); (ii) a specific 'refuge' within the major food groups; (iii) an effective spatial separation by the action of the current/substratum, i.e. within the shallow-gradient streams there are regions of 'harsher' conditions to which only *Crenobia alpina* would have access. Of these possibilities the second one would be the easiest to test (by the production of specific antisera) but the first and the last would present considerable technical difficulties.

ACKNOWLEDGMENTS

SUMMARY

(1) The evidence for interspecific competition between *Crenobia alpina* and *Polycelis felina* (Tricladida) in the spring-fed streams of North Wales is examined.

(2) Circumstantial evidence is presented on the basis of distribution and abundance.

(3) Using serology, it was demonstrated that their food requirements were very similar, thus providing a basis for competition.

(4) Evidence of intraspecific competition from the performance of field populations could not be obtained. However, a relative increase of the food resource by manipulating the population resulted in the apparent alleviation of intraspecific competition as determined by a biochemical method.

(5) Finally, a natural experiment presented itself whereby a sudden decrease in a numerically superior population of *P. felina* resulted in a rapid increase in the numbers of a previously numerically inferior population of *Crenobia alpina*. This was considered good evidence of interspecific competition.

(6) It was concluded that collectively the several approaches suggested that interspecific competition was occurring between the two species.

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