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**Aspects of the ecology of the palmate newt (*Triturus helveticus*)
in the Flow Country of Sutherland**

by

David Rees

A dissertation submitted in partial fulfillment of the requirements
for the degree of Master of Science in Advanced Ecology

Biological Sciences

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- 6 NOV 1995

SUMMARY

- (1) Aspects of the ecology of the palmate newt, *Triturus helveticus* (Razoumowski) were studied in pool complexes on blanket bog in Sutherland. The impacts of coniferous afforestation of blanket bog on *T. helveticus* were assessed through the selection of pool complexes surrounded by trees, as well as unplanted complexes.
- (2) Aquatic invertebrates were sampled in each of the 188 pools involved in the study, in order to determine possible associations of invertebrate families with *T. helveticus*. For each pool, water pH, temperature and depth were measured, as well as an estimate of the perimeter of the pool. Two sets of amphibian surveys were carried out, 20-23rd of May and 25-28th June 1994.
- (3) No species of newt other than *T. helveticus* was found on either of the two surveys. *Triturus helveticus* was found mainly in the deeper pools, and there was also a preference for pool types with abundant aquatic vegetation. Analyses of the invertebrate data using DECORANA and CANOCO showed that several families respond to the same environmental variables as newts, including *Chaoboridae* (pupae), *Libellulidae*, *Coenagriidae*, *Gyrinidae*, *Corixidae*, and *Chironomidae*.
- (4) Many larval newts were caught during the first survey, and these were taken to be individuals which had failed to metamorphose in their first year and subsequently overwintered in the water. Pools pH was found to be low (3.99-4.43) and this is likely to reduce the rate of larval development. Tadpoles and eggs were not found until the second survey, suggesting that breeding in the current year did not start until mid-June.
- (5) The mean sizes for adult male newts was 67mm and for females, 73mm. Mean sizes of newt larvae were 33mm in the first survey and 36mm in the second survey. The mean size at metamorphosis was found to be 39mm, from overwintered newts caught in terrestrial pitfall traps between June and August.
- (6) *T. helveticus* was present on all four pool complexes, suggesting that coniferous afforestation does not adversely affect this species in the short term, and in the long term may improve the habitat for *T. helveticus* during the terrestrial phase by providing additional refugia.

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1. 0 INTRODUCTION

1.1 The Flow Country

The highly Atlantic climate of northern Scotland has allowed the development of extensive low level moorland, almost down to sea level. These conditions have led to a northern tundra type ecosystem developing in a southern geographic and climatic location (Stroud, *et al* 1987). The extensive tracts of peatland which cover much of Caithness and Sutherland represent perhaps the largest single expanse of blanket bog in the world. This area is of major importance on both a national and an international scale due to the global scarcity of this habitat.

'Flows' are flat or nearly flat areas where deep peat has formed. These areas have a high degree of intricate surface 'patterning', with complex pool formations developing in many places (Lindsay, *et al* 1988). The 'Flow Country' is a term now applied to describe the whole peatland area in Caithness and Sutherland. The highly Atlantic climate has greatly influenced plant distribution and vegetation development in this area, resulting in unique vegetation assemblages (Stroud, *et al* 1987).

These ecosystems represent a relatively undisturbed natural post-glacial climax. As well as containing unique assemblages of plants, the Flow Country is of great value as a feeding area for wetland birds. The blanket bogs of Caithness and Sutherland support a high diversity of bird species, including large populations of breeding waders (Lindsay, *et al* 1988).

The ecology of amphibian species in the Flow Country is less well understood.

The continued existence of parts of the Flow Country is threatened by coniferous afforestation. By 1987, 67,000 ha (17%) of the original peatland area of Caithness and Sutherland had been planted or approved for planting (Lindsay, *et al* 1987). Coniferous afforestation leads to a transformation of the peatland ecosystem through disruption of the water table and resultant changes in vegetation composition. Smith and Charman (1988) demonstrated that even minor reductions in the level of the water table cause alterations in the occurrence of ombrotrophic mire species. The effects of afforestation on these complex ecosystems may irreversibly alter the nature of the Flow Country.

1. 2 *Triturus helveticus* (Razoumowski) and the British newts

Three species of newt occur in Britain; the smooth newt (*Triturus vulgaris* (L.)), the great crested or warty newt (*T. cristatus* (Laurenti)) and the palmate newt (*T. helveticus* (Razoumowski)) (Denton, 1991). The palmate newt occurs more in soft-water ponds than the smooth newt, and the distribution patterns of the two species appear to be related to geology (Cooke and Frazer, 1976, Griffiths, de Wijer and Brady, 1993). *Triturus helveticus* and *T. vulgaris* are very similar in terms of general morphology, feeding and microhabitat selection (Griffiths, 1987), but the two species appear to be separated by water quality. All three species coexist in certain ponds, although *T. vulgaris* and *T. cristatus* are rarely found in pools with a pH below 6.0 while *T. helveticus* can tolerate pH as low as 4.0 (Cooke and Frazer, 1976). The smooth and warty newts have almost identical distributions in Britain, and warty newts are rarely found in the absence of smooth newts (Cooke and Frazer, 1976).

Bell and Lawton (1975) describe the palmate newt as a small carnivorous poikilotherm. Like all other newts, *T. helveticus* returns to the water to breed and has aquatic larvae. Although mainly seen in the water, newts spend a considerable part of their lives on land. At metamorphosis, larvae lose their external gills and begin a period of land habitation. Juvenile newts remain on land until sexually mature. Maturity is reached after a period of between two and seven years (Frazer, 1983), and following this, adult newts return to water each year to breed. Newts normally emerge from hibernation and migrate to water to breed in March or April (Frazer, 1983).

Each female deposits 100-500 eggs (Miaud, 1993) over a period of 1-3 months. Frazer (1983) states that the British newts lay their eggs singly in aquatic vegetation. Eggs are often wrapped in leaves, with the egg membranes acting as an adhesive. Wrapping of eggs is thought to occur in an attempt to reduce predation (Bell and Lawton, 1975). At metamorphosis the gills are lost but the tail is retained. Newt tadpoles are wholly carnivorous, feeding initially on small invertebrates and later taking larger prey such as the tadpoles of frogs and newts (Frazer, 1983).

The rate of development is dependent on factors including pH, water temperature and food availability, but metamorphosis is normally reached in two to three months (Frazer, 1983). In unfavourable conditions metamorphosis may be delayed until the following

year, and van Gelder (1973) found that many larvae regularly overwintered in pools in the Netherlands.

On land, hibernating adults and juveniles utilise refugia such as stones and cracks in the ground. During hibernation, newts are at risk from freezing. Wet ground must also be avoided, and newts on land are susceptible to desiccation.

Adult male palmate newts are significantly smaller than both the warty and the smooth newt, but female smooth and palmates are of a similar size. Male palmates are easily distinguished from smooth and warty newts by their characteristic filament at the tip of the tail and also by strongly webbed hindfeet. These are sexual features which vary from season to season (Smith, 1973). Female palmates can normally be distinguished from those of *T. vulgaris* by the absence of spots from the throat. The larvae of smooth and palmate newts are indistinguishable until just before metamorphosis, when palmates become pink or brown on the ventral side (Frazer, 1983).

1.3 Aims

The present study is an investigation of aspects of the ecology and habitat characteristics of *T. helveticus* in the Flow Country. Published work has been found to be lacking on *T. helveticus* in the Flow Country. Recent studies have brought to light potentially important effects of low pH on the development and feeding ability of both smooth and palmate newts (Griffiths, 1993, Griffiths, de Wijer and Brady, 1993). One of the aims of the present study was simply to confirm the presence of *T. helveticus* in pool complexes of the Flow Country, given the acidic conditions associated with blanket bog. The Flow Country represents a habitat unlike any other, and another aim of the present study is to investigate the types of pools selected by newts as breeding habitat, primarily in terms of size and depth, but also with regard to their associations with aquatic invertebrate families which contain both potential prey and predators.

2. 0 METHODS AND MATERIALS

2.1 Study areas and site selection

All sites included in this study are located in blanket bog complexes in east Sutherland. Sites were chosen that offered a representative sample of the different pool types present in the area. The sites had a relatively low diversity of terrestrial plant species and vegetation over the sites appeared to be fairly uniform. To allow an assessment of the impact of afforestation on palmate newts, two pool complexes were chosen in a forested area. Two other study sites were established on an area of blanket bog containing several pool complexes. These complexes were separated by areas of wet ground without discrete pools and were thus treated as individual sites.

2. 1. 1 Loch-nan Clar

Two study sites were located on an area of blanket bog adjacent to Loch-nan Clar. This area contains several complexes of pools, and two were chosen which possess the range of pool types supported by the area as a whole. These sites will be referred to as Loch-nan Clar (LNC) I and II from now on. The complexes chosen at LNC I (grid reference NC 776378) and LNC II (grid reference NC 780379) appeared to differ little in terms of the range and physical structure of the pools they contained. LNC II, at 150-160m above sea level, is at a slightly higher altitude than LNC I at 140-150m . The Loch-nan Clar sites both

contained a visually distinct core to the pool complexes, with well developed Dubh-lochs (the D pools) at the centre, many shallow interconnected pools at the periphery. The Loch-nan Clar blanket bog system has been designated as a Site of Special Scientific Interest.

2. 1. 2 Woodcock Hill

The principle difference between the pool complexes at Woodcock Hill and those at Loch-nan Clar is the fact that the former are surrounded by plantation forestry of various ages. The remaining pool complexes on this site survive in their present form only because they are areas which are too wet to plant with conifers. This means that the extent of the pool complexes is dictated by the surrounding forestry and drainage ditches. Both Woodcock Hill complexes are surrounded on all sides by conifer plantations of various ages (though

one edge of W II is bounded by a stream before the plantation begins) and the associated drainage ditches. The first site to be established at Woodcock Hill (W I) is located at grid reference NC 900474, and the second (W II) at grid reference NC 893468. The two Woodcock Hill sites again differ in altitude, with W I at 110-120m above sea level and W II at 140-150m. The lower site, W I was the smallest of the four pool complexes included in this study, although it contained all the same pool types (see Table 1) as found on LNC. W II, however, differed from the other three sites in as much as it only contained pools of one type only.

2. 2 Classification of Pool Types

Several readily recognisable pool types can be found in the complexes on the sites included in this study. Differing pool types found in the flow country have been described by Ratcliffe and Oswald (1988), and a more detailed pool classification has been carried out in east Sutherland by Twiss, Thomas and Evans (1993). The latter classification of the peatland habitat is based largely on the physical structure of the pool types and the areas between pools. The categorisation developed by Twiss *et al* (1993) was used in this study as it provided a convenient framework within which to consider habitat utilisation by palmate newts during their aquatic phase. The pool types from this classification which were encountered during this study are described below (taken from Twiss *et al*, 1993)

2. 2. 1 Pool Type 'A'

In A type pools, the sphagnum surrounding the pool slopes gently into the water and there is no distinct edge. These pools are often choked with sphagnum and appear shallow, with a clear water column depth often only 5-15cm. These pools can be deep, with a layer of floating sphagnum over a suspended peat pool base. Pools of type A tend to be of a linear form, 1-2m wide and up to 20m long, and are often found lying parallel to slope contours on gentle slopes surrounding complexes of D type pools (see below). The sphagnum carpet surrounding these pools is usually wet with few raised hummocks.

2. 2. 2 Pool Type 'B'

These are small (<2m²) irregular shaped pools. The pool bed consists of bare peat and is generally free of vegetation. These pools are shallow (5-10cm) and the pool bed is sufficiently solid to stand upon (unlike other pool types). There is no distinct edge to this

pool type, with vegetation or bare peat sloping irregularly into the pool. These pools appear to be susceptible to drying out (equivalent to microform A2, Ratcliffe and Oswald, 1988). The ground between the pool is very irregular and broken with hummocks of sphagnum covered in thick growths of *Racomitrium lanuginosum* (microform T3, Ratcliffe and Oswald, 1988). Pools of this type generally occur on slopes surrounding D type pools and there is often a distinct step in elevation from B pools to D pools.

2. 2. 3 Pool Type 'D'

These are Dubh-lochs proper, and are generally found at the centre of a pool complex, usually on a flat gradient such as the apex of a raised mire. These pools are large (>2m²) and have a distinct vertical edge. D pools are equivalent to microform A4 in Ratcliffe and Oswald, 1988. These pools are irregularly shaped, often with small islands or promontories where adjacent pools have joined. The clear water depth is greatest around the edges of these pools, and is approximately 10-30cm, below which is a deep layer of suspended peat particles. Pool vegetation is primarily *Eriophorum angustifolium* and *Menyanthes trifoliata*. The narrow areas between the pools of this type is often relatively dry, but formed of a thick layer of sphagnum. Pools at the periphery of the group occasionally drain or dry out (equivalent to microform A3 in Ratcliffe and Oswald, 1988).

2. 2. 4 Transitional areas and intermediate pool types

The categorisation of Twiss et al (1993) classified areas of peatland by the pool types contained within them. In addition to this, transitional areas between pool types were also recorded, such as A/B. Such areas contained mixtures of pool types within the immediate vicinity of the observer, but graded into more discrete types (Twiss *et al*, 1993). However, the present study involved the classification of individual pools, rather than of areas of pools of one type or another.

As well as the three main categories of pools described above, many pools exhibited characteristics of more than one of these types. In most cases, the selection of the pool type which most closely matched was acceptable. The one exception which occurred was with some pools which were partly D and partly A, i.e. pools which were partly steeply edged and with little vegetation, and partly shallow, choked with vegetation, and with gently sloping edges. Such pools were labelled as AD's, but this is the only alteration made to the original classification. Further subdivisions could have been made, e.g. AB,

but it was considered that these pools were not sufficiently different from the pure A or B type to warrant a new category.

2.3 Methodology

2.3.1 Sampling method

Two parallel transects, 40 metres apart, were established on each of the four sites using a compass. These were marked out between 23rd and 28th of April 1994 using 1.5-2.0 metre canes to aid relocation. The transects took the form of cross-sections, from start to finish, across the pool complexes. The extent of the Woodcock Hill sites was dictated by the extent of the forestry. In the case of the less discrete Loch-nan Clar complexes, transects began and ended in areas on the periphery of the main pool complex, where no further variation in pool type occurred.

Each pool intersecting with a transect was included in the study, with a total of 188 for all sites. The number of pools on each transect is shown in table 1.

Site	Transect	Number of Pools
LNC I	A	23
	B	27
LNC II	A	17
	B	22
W I	A	24
	B	21
W II	A	28
	B	27

Table 1: Numbers of pools on each transect

2.3.2 Pool variables

Working transect by transect, for each pool included in the study, the following variables were recorded:

- (i) Pool number along the transect. Individual pools were only marked in cases where the pool did not obviously lie along the line of the transect, and this step was taken mainly to aid relocation.
- (ii) Pool type, according to the classification described in 2.2 was also recorded, as this instantly provides a picture of the main characteristics of the pool.
- (iii) Depth of water was measured at the pool edge, to the nearest centimetre.

(iv) pH and temperature were measured using a Jenway 3150 waterproof pH meter. These were recorded both in the morning (0900 - 1030 hrs) and in the evening (1730 - 1900 hrs) at the water surface at the edge of the pool. In pools over 8cm deep, pH and temperature were also measured at the bottom of the water column.

(v) The perimeter of each pool (the amount of 'edge' in metres) was estimated by pacing out. Islands were omitted from this estimate. Some pools were classed as 200m+ or 300m+, these taking too long or being too dangerous to pace out completely.

(vi) Aquatic vegetation in each pool was also surveyed and recorded according to the DAFOR scale. Plants growing in the pool itself or just below the water level at the pool edge were included in these surveys.

(vii) A sample of water was collected from ten pools per transect and this was later tested in the lab for Calcium hardness. This method was discarded as the Calcium levels in the samples proved too low to be recorded reliably.

2.3.3 Invertebrates

In order to assess the invertebrate fauna of the study pools, invertebrate surveys were carried out between the 24th and 28th of April for LNC and W I, and on the 18th to 19th of May for W II. The National Pond Survey method of sampling invertebrate fauna was not adopted. This method involves a total of three minutes sampling divided between different microhabitats. Some of the pools in this study were very large, and others were felt to be too small for this method to be used efficiently. A standard sampling method was therefore devised, with one figure of eight sweep made with a long-handled pond net per 2m of edge, up to a maximum of 20 sweeps per pool. Searches were concentrated at the edges of pools and in large pools the sampling was divided to allow as many microhabitats as possible to be included. The contents of the net were placed into a plastic tray and the invertebrates removed with forceps and then placed in 70% alcohol. Invertebrates were later identified to family level in the laboratory.

2.3.4 Amphibians

A separate set of surveys was carried out for determining the presence of amphibian species. A similar standard sampling regime was used to that involved in invertebrate sampling. Again, pool size was incorporated into the sampling method and therefore one minute was spent searching for amphibians per 2m of edge, up to a maximum of 20 minutes. This allowed the most effective methods to be employed and decisions made on

a pool by pool basis. In pools with large perimeters, random sweeps alone did not prove effective in showing the presence of newts. In larger pools with relatively little vegetation, the most effective method for catching adult newts proved to be a combination of 'stalking' and random sweeping. In pools with much aquatic vegetation, stalking yielded very few newts due to the abundance of cover, and so in these cases random sweeping proved to be the most effective sampling technique. For locating newt larvae, random sweeping proved to be the only adequate method.

Trials were made with water traps (described in Griffiths, 1987a) but these did not prove to be a satisfactory method of establishing newt presence or absence. The effectiveness of this technique was found to be limited by the absence of aquatic vegetation in many pools. Even in pools where newt presence had been established by netting, newts were not captured in water traps left overnight. The relatively low numbers of these traps that were available meant that only two pools could be sampled at a time. Griffiths (1987a) suggests that 12 traps per pool are needed to establish newt presence. To survey one transect in this manner would therefore require the use of up to 336 traps. Unless pools could be isolated, perhaps by surrounding them with polythene sheeting, a transect would have to be surveyed in one attempt to ensure that the same newts were not being caught in different pools at different times. Sampling with water traps is also time consuming, as traps should preferably be left overnight (Griffiths, 1987a). These factors, coupled with the low effectiveness, led to the establishment of the technique described above.

Amphibian surveys were carried out between the 20th and 23rd of May, and again between the 25th and 28th of June. During sweeping and stalking in each pool, presence of frog tadpoles was noted and any newts caught were removed and placed temporarily in a plastic tray. Adult newts were then identified and sexed before their length was measured. Adult and larval newts were measured from the tip of the snout to the end of the tail, and also from the tip of the snout to the end of the cloaca, as described in Harrison, Gittins and Slater (1983a). In adult palmate newts, the tail filament was excluded from measurements as this is a sexual feature and varies in length from season to season (Smith, 1973). Measurements were taken by placing the newts on a notebook and marking the positions of the above features using a pencil. This method was devised following trials with sheets of acetate and amounted needle, which was unsatisfactory in windy conditions. In all cases, newts were handled with care and returned to the pools they were found in as quickly as possible. All measurements were taken to the nearest millimetre.

The terminology used in the present study to describe the various stages of newts are as follows:

- (i) Eggs. Laid singly, usually on aquatic vegetation by female newts
- (ii) Tadpoles. This refers to newly hatched larvae
- (iii) Larvae. Tadpoles develop into larvae, retaining external gills. In the year of hatching, larvae may be referred to as first year larvae. Second year larvae result from first year larvae failing to metamorphose in their first year
- (iv) Juveniles. External gills are reabsorbed at metamorphosis, and at this stage larvae become juveniles. Again, first or second year juveniles result from larvae reaching metamorphosis in their first or second year
- (v) Adults. After spending a period on land, juveniles reach sexual maturity, and at this stage they become adults.

2. 3. 5 Vegetation

On the same dates as the transects were established, terrestrial vegetation was sampled in order to assess differences between sites. This was carried out by using five 2x2 metre quadrats placed at random along the length of each transect. Presence and abundance of each plant species within each quadrat was recorded according to the domin scale, and these data were later applied to the Tablefit programme to determine the NVC classification of each site.

2. 4 Multivariate analysis

2. 4. 1 TWINSPAN

Classification of the invertebrate data collected for each pool was carried out using TWINSPAN (two-way indicator species analysis). This is a polythetic divisive technique where data is ordinated by reciprocal averaging. The samples are divided into clusters and a corresponding species classification is produced (Hill, 1979a). Samples and species are displayed as a dendrogram. TWINSPAN uses pseudospecies rather than the species themselves to denote abundance values, and pseudospecies cut levels are chosen to divide the chosen scale of abundance into segments. In this case, a log scale was chosen for cut levels as many families were absent from many samples and low numbers were common. Four cut levels were set, at 0, 1, 10 and 100.

Species are ordered along a principal axis by reciprocal averaging and indicator species are chosen, i.e. those species which show a clear preference for one side of the division or the other. The division is made near the middle of the axis and the process is repeated on each new group formed until no further divisions can be made. In this case, the number of divisions was limited to three, as the aim was to split the samples into four main groups in an attempt to relate these to the pool classification of Twiss *et al* (1993). The samples in each final cluster could then be referred to the original data to determine the pool type attributed to each pool in the initial survey.

2. 4. 2 DECORANA

DECORANA (detrended correspondence analysis) is an eigenvector ordination technique based on reciprocal averaging. The principal axes of variation within the data set are extracted and an ordination diagram is then produced for species and sample scores, which sets similar species or samples close together, and dissimilar ones are set apart (Hill, 1979b).

2. 4. 3 CANOCO

Canonical correspondence analysis attempts to explain variation in data by ordination axes that are constrained to be linear combinations of environmental factors (Ter Braak, 1988). Environmental biplots are produced which ordinate the species or samples and represent environmental variables as arrows. The degree of contribution the the principal axes are indicated by the length and direction of the arrows.

3. 0 RESULTS

3. 1 Characteristics of vegetation and pools

3. 1. 1 Vegetation

Terrestrial vegetation

Terrestrial vegetation data for the two transects on each of the four sites were amalgamated, as any potential differences between sites were felt to be of greater importance than differences within sites. Using the data in the TABLEFIT program (Hill, 1993), all four sites were found to fall into the *Scirpus cespitosus* - *Eriophorum vaginatum* blanket mire category (M17b) of the NVC. Goodness of fit values ranged from 73 to 82.

Aquatic vegetation

Vegetation in the pools themselves was recorded according to the DAFOR scale. This data is available in Appendix 1. The classification of pools according to their physical and vegetation characteristics by Twiss *et al* (1993) was adopted in the present study. The characteristic vegetation of D type pools is impoverished, but includes *Menyanthes trifoliata*. This species consists mainly of long stems. Leaves and flowers are elevated above the water surface, and so this species is not likely to provide cover for newts or eggs. D pools may have species of *Sphagnum* growing at the edges, or in shallow areas, but rarely in the deeper parts of the pool.

B type pools are shallow and tend to have little vegetation. The pool bottom is usually bare peat, and the tendency for desiccation of B pools allows species such as *Myrica gale* to grow in these pools. A pools are characterised by an abundance of aquatic vegetation, notably various *Sphagnum* species. A pools are often choked by vegetation and are sometime shallow. Large, deep pools which retained other characteristic features of this pool type were found on W II. Also, some pools found on most sites exhibited characteristics of both A and D pools, being deep and well defined, but having abundant vegetation in much of the pool.

Pool Type					
Site	B	A	D	AD	Total
LNC I	22	11	13	4	50
LNC II	12	6	11	9	38
W I	6	24	10	5	45
W II	0	55	0	0	55
Total	40	96	34	18	188

Table 2: Distribution of pool types between sites.

3. 1. 2 Pool type distribution

An analysis of differences in the distribution of numbers of pool types on the four sites (see Table 2) yielded a significant result (Chi-square = 98.428, 9df, $P < 0.005$). This result is not surprising given the total absence of all pools except type A on site W II. Two of the expected values in this test were less than five and so this result should be treated with caution. However, a further test on differences in pool distribution excluded this site and still gave a significant result (Chi-square = 23.481, 6df, $P < 0.005$). Relatively few A type pools were contained in the transects on LNC, but these sites had a greater number of B and D type pools than W I. Overall, the most common pool type was A, followed by the shallow B type pools. There were fewest examples of D and AD pools, respectively.

3. 1. 3 Pool variables

Using the recorded pool variables of depth, edge, temperature and pH, the plots shown in Figures 2 to 4 were produced. All plots involving temperature or pH were done on a transect by transect basis, as these measurements were taken on different days. Even though the transects on each site were only 40m apart, the influence of environmental factors on pH and temperature could not be ruled out and so data could not be pooled. The measurements used in the production of these plots and later analyses were those taken from the top of the water column in the morning.

Pool depth

The pool depth on most sites did not exceed 35 cm. Loch-nan Clar I contained deeper pools than all other sites, with pools up to 37 cm on LNC IA and up to 55 cm on LNC IB. LNC IB was also the site with the smallest maximum pool size, 72 m, compared with between 165 m and 300 m on all other sites. Figures 1 to 3 show that there is generally a tendency for pool depth to increase with pool size (the amount of edge). This pattern is illustrated to a lesser or greater extent on all transects on all sites, and can be seen in the

Figure 1: LNC IA relationship of edge and depth

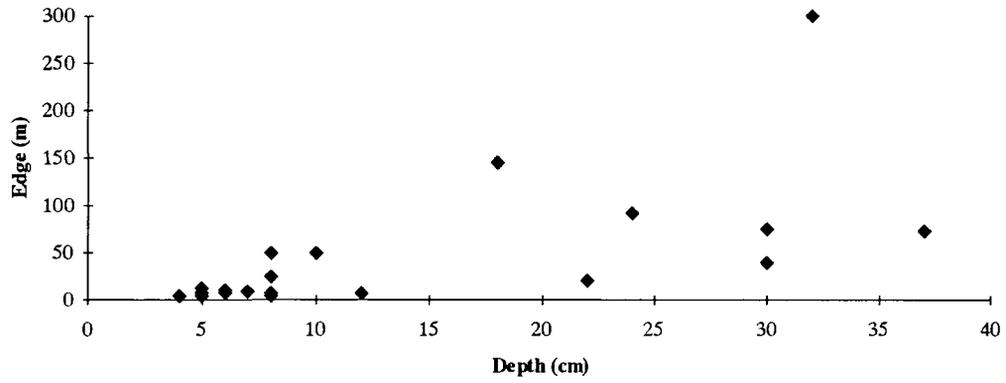


Figure 2: LNC IB relationship of edge and depth

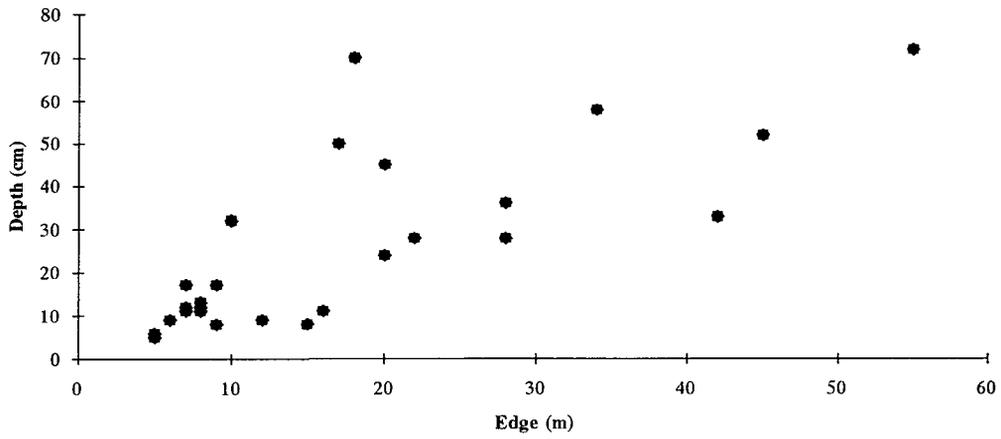
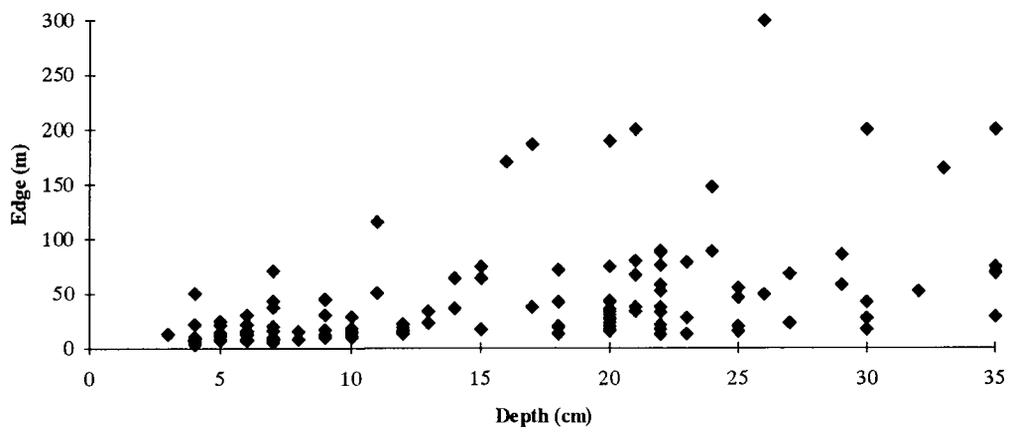


Figure 3: Depth / edge LNC II, W I, W II



graphs in Appendix 2. The very largest pools, those classed as 200 or 300 m are not necessarily the deepest. Large pools often form when two adjacent pools join, and so the depth can remain the same as that of much smaller pools.

Pool type	Mean	SD	n
A	12.71	6.65	96
AD	25.89	5.80	18
B	6.65	2.30	40
D	27.76	8.12	34

Table 3: Mean depths by pool type.

Temperature

The minimum and maximum temperatures for the eight transects are shown in Table 3. Although caution must be exercised when interpreting these data, it appears that W II has lower temperatures than the other sites. It is possible that the relatively high altitude of this site accounts for this result. When looking at the relationship between temperature and the depth of a pool, a general picture of decreasing temperature with increasing depth emerges. There appears to be a similar relationship when temperature and the amount of pool edge are examined. Appendix 2 contains plots of both edge and depth against temperature. The lower temperatures might be expected as larger, deeper pools would heat up more slowly during the day than small shallow pools.

	LNC I		LNC II		W I		W II	
(°C)	A	B	A	B	A	B	A	B
Max	15.9	10.9	12.1	16.2	12.1	11.6	9.9	9.0
Min	11.7	9.3	10.0	11.1	8.7	9.1	7.7	6.1

Table 4: Minimum and maximum temperatures (am, top) for all transects.

pH

The minimum and maximum pH values recorded are contained in Table 4. From this it appears that as well as being the site with the lowest pool temperatures, W II has the lowest pH values also. The remaining three sites are all relatively similar, although the minimum values for W I are slightly lower than those found on the two LNC sites.

Analysis of pH values in relation to edge and depth resulted in the series of plots found in Appendix 2. Here again there is some suggestion of a relationship between these factors, with deeper, larger pools tending to have higher pH values. Looking at the plots of edge, in some cases pH is only marginally higher (e.g. LNC IB) and if some of the outlying

points are removed the relationship is lost. The plots involving depth seem to show a more definite pattern, with clusters of larger pools with higher pH values occurring (e.g. LNC IIB).

	LNC I		LNC II		W I		W II	
pH	A	B	A	B	A	B	A	B
Max	4.43	4.34	4.36	4.38	4.26	4.38	4.17	4.15
Min	4.13	4.06	4.16	4.06	4.04	4.04	3.99	3.99

Table 5: Minimum and maximum pH values (am, top) for all transects.

The pH values for the am and pm measurements do not generally differ greatly. Plots of these values are located in Appendix 2. In most cases the pH value taken in the evening exceeds the am value, but there is often some degree of overlap in the pools at the extremes of the transects, where shallow pools are most common. In some cases (LNC IB, LNC IIA and W IIA) all evening pH values are greater than those in the morning. Another pattern which appears to exist on some transects is that the higher pH values are found towards the centre of the cross-section. However, this may be because the larger, deeper pools associated with this part of the pool complex possess a higher pH than the surrounding pools.

The data collected on temperature differences between the start and end of the day show that the pools generally become warmer through the day, on W IA there is a difference of almost 6°C from morning to evening. Other areas show smaller differences (e.g. LNC IIA differs by around 2°C) but the pattern is similar. In several cases, the am temperature is greater than the pm temperature in pools at the extremes of the transects. This may be due to the shallow pools warming up very quickly in the morning, and subsequent rapid cooling in the evening. The plots obtained from the temperature data can be found in Appendix 2.

3. 1. 4 Differences between the wooded and non-wooded sites with respect to pool variables

The pH and temperature data collected were used to test for broad differences between the Loch-nan Clar and the afforested site. The morning readings taken at the water surface were used rather than readings from the evening or from the bottom of the water column. This was done mainly because following the morning readings, sampling for

invertebrates took place, and inevitable disturbance of the pool could perhaps have affected the later readings.

Site	Mean	Std Dev	Minimum	Maximum	N
LNC pH	4.22	0.09	4.06	4.43	88
W pH	4.11	0.07	3.99	4.38	100
LNC Temp (°C)	11.71	1.90	9.30	16.20	88
W Temp (°C)	8.92	1.43	6.10	12.10	100

Table 6: Mean, minimum and maximum temperature and pH for LNC and W.

Before testing for differences in temperature and pH between the two areas, a Kolmogorov - Smirnov goodness of fit test was applied. The results of this test for both pH and temperature for both areas showed that the data did not differ significantly from the normal distribution. Following this t-tests for independent samples were performed, which gave highly significant difference between the two areas (pH t-value = 9.83, 186 df, $P < 0.000$; temperature t-value = 11.46, 186 df, $P < 0.000$). This result reflects the small variation around the mean pH value for each of the two sites, as shown in Table 6. Although the mean values are close (diff. = 0.11), there is only a small degree of overlap between the values of the two areas. In the case of temperature, there is more variation about the mean values than in the case of pH, but there is a greater difference (2.79 °C) between the mean values themselves, and this may explain the significant result.

3. 2 Invertebrate data

3. 2. 1 TWINSPAN analysis

All pools included in the study were classified on the basis of their invertebrate composition using TWINSPAN (Hill, 1979a). This was done in an attempt to deduce whether the invertebrate fauna of pools reflected the classification made by Twiss *et al* (1993) on the basis of physical variables such as depth, size and vegetation. The invertebrate data was ordinated using TWINSPAN in order to investigate whether the pool types recognised by the classification of Twiss *et al* (1993) could be shown to have characteristic suites of invertebrate families. In this way, it was hoped to show whether a certain group of invertebrate families would be common to all B type pools, another would be representative of A pools and so on. Newts and frog tadpoles were also retained in the data set for this analysis.

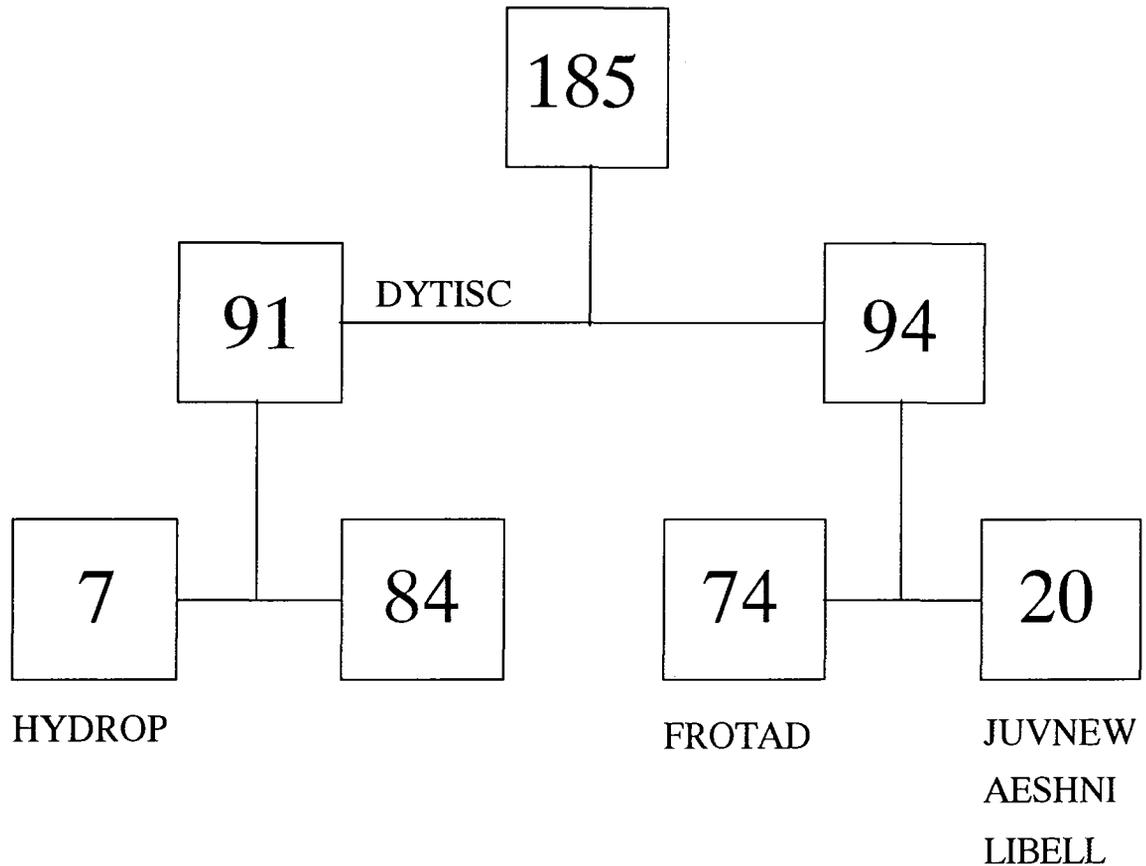


Figure 4: Dendrogram representing the major divisions of a TWINSpan classification of the pools according to their aquatic invertebrate composition. Figures in boxes are the number of samples in each subdivision. Indicator species codes are given in Appendix 3. Negative indicator species are shown on the left of each division and positive indicators to the right.

The results of the TWINSpan classification of the pool invertebrate data are presented in the form of a dendrogram (Figure 4). Four final groups were recognised by this technique. The first division splits the samples almost symmetrically, primarily on the basis of the presence or absence of members of the *Dytiscidae*. In this first split, 91 samples are allocated to one group, and 94 to the other. *Dytiscidae* is the only indicator species here, and no indicators for the other group were given. In the next division, again, there was only one indicator species (again negative), this being *Hydrophilidae*. This division allocated 92% of the samples in group 91 into one group and the remaining 7% to another. In the third and final division illustrated in Figure 4, 79% of the samples in group 94 were allocated to one group. The indicator species for this split were frog tadpoles for the larger group, and newt larvae along with the families *Aeshnidae* and *Libellulidae* for

the smaller group. After three divisions, 85% of the samples are still clustered into two groups (84 and 74). This suggests that the overall invertebrate community is fairly homogeneous and the smaller clusters formed represent less common fractions of the community.

Group	B	A	D	AD
7	1	5	1	0
84	9	35	23	10
74	22	39	8	4
20	9	6	3	1

Table 7: Numbers of each pool type allocated to the four main TWINSPAN groups.

The final four groups presented in the dendrogram in Figure 4 were analysed to determine which samples (pools) were placed into which groups. Table 7 shows the number of each pool type placed into each of the final groups. From this the proportions of each pool type placed in each group was determined.

Group 84 contained 67% of AD type pools, and 66% of Ds. This suggests the group consists mainly of deeper pools. This group also contains a large proportion of A pools, although 77% of these are located on the woodland sites, where many deep A pools were found.

The group containing 74 samples contained 54% of the B pools and 46% of A pools so it seems likely that this group contains the more shallow pools. The remaining two groups contain only a small number of pools of different types. Group 20 contained almost 50% B pools and group 7 contained 71% A pools.

The results of the TWINSPAN classification reveal that the final groups are in no instances composed purely of pools of one type. Each group contains a mixture of pool types which were found to be similar on the basis of the invertebrate fauna they contained. Although no clusters of single pool types occurred, this is perhaps to be expected in a natural system which is as variable and complex as are these blanket bog systems.

The classification shown in Figure 4 was taken a stage further, but this next division has not been shown as it was not found to be helpful in summarising the data. One thing which did emerge from the seventh division (of group 20), however, was a split in the samples which took a greater proportion of the samples away from the centre of the

division than in previous divisions. Until this point, samples had tended to be clustered around the centre of the division, suggesting a high degree of similarity.

3. 2. 2 Detrended correspondence analysis

The same invertebrate data was further analysed using DETrended CORrespondence ANALysis. The data was subjected to a log transformation and rare species were downweighted. Samples 10 and 11 were omitted from the analysis, as no invertebrates or newts were recorded in these pools. Outliers were removed and then replaced when it was discovered that their exclusion did not increase the spread of the data. The eigenvalues of the four principal axes of variation extracted by DECORANA are given in Table 8. The higher the eigenvalue, the more important the ordination axis. It can be seen that the first two axes contribute to most of the variation, whereas axes three and four are of much less importance. Another thing to emerge from the examination of these values is the fact that axis one accounts for almost four times the amount of variation as the second principal axis.

Ordination axis	Eigenvalue
1	0.51281
2	0.13644
3	0.11213
4	0.09139

Table 8: Eigenvalues for the four principal axes extracted by DECORANA.

Figure 5 shows a DECORANA ordination of the invertebrate family scores along the first and second principal axes of variation. Codes for the families are given in Appendix 3. Families at the extremes of the two axes are not important in the analysis, as these were recorded very rarely and so contribute little to overall trends. Families that fall into this category include *Coleoptera* larvae and *Culicid* type.

Figure 5 shows a group of families clustered together on the negative end of the first principal axis. This group seems fairly neutral in terms of the second principal axis, and includes juvenile and adult palmate newts, newt tadpoles and the families *Aeshnidae*, *Libellulidae*, *Coenagriidae* and *Gyrinidae*. In the course of field work it was observed that these are all families associated with the deeper pools encountered in this study.

On the positive side of the first principal axis no clusters of families occur, but there is a wide spread along the second principal axis. Many of these are families encountered

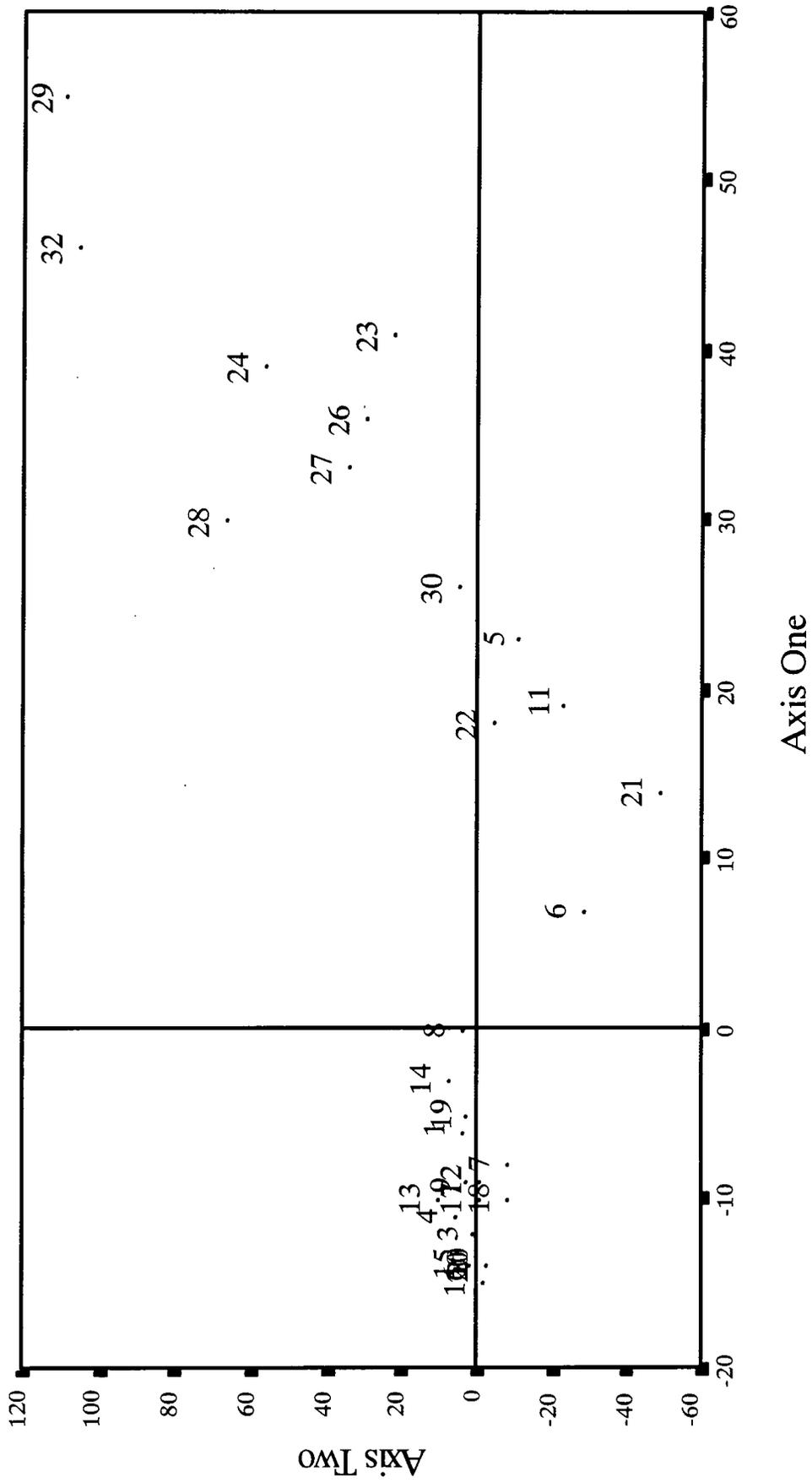


Figure 5: DCA ordination of families

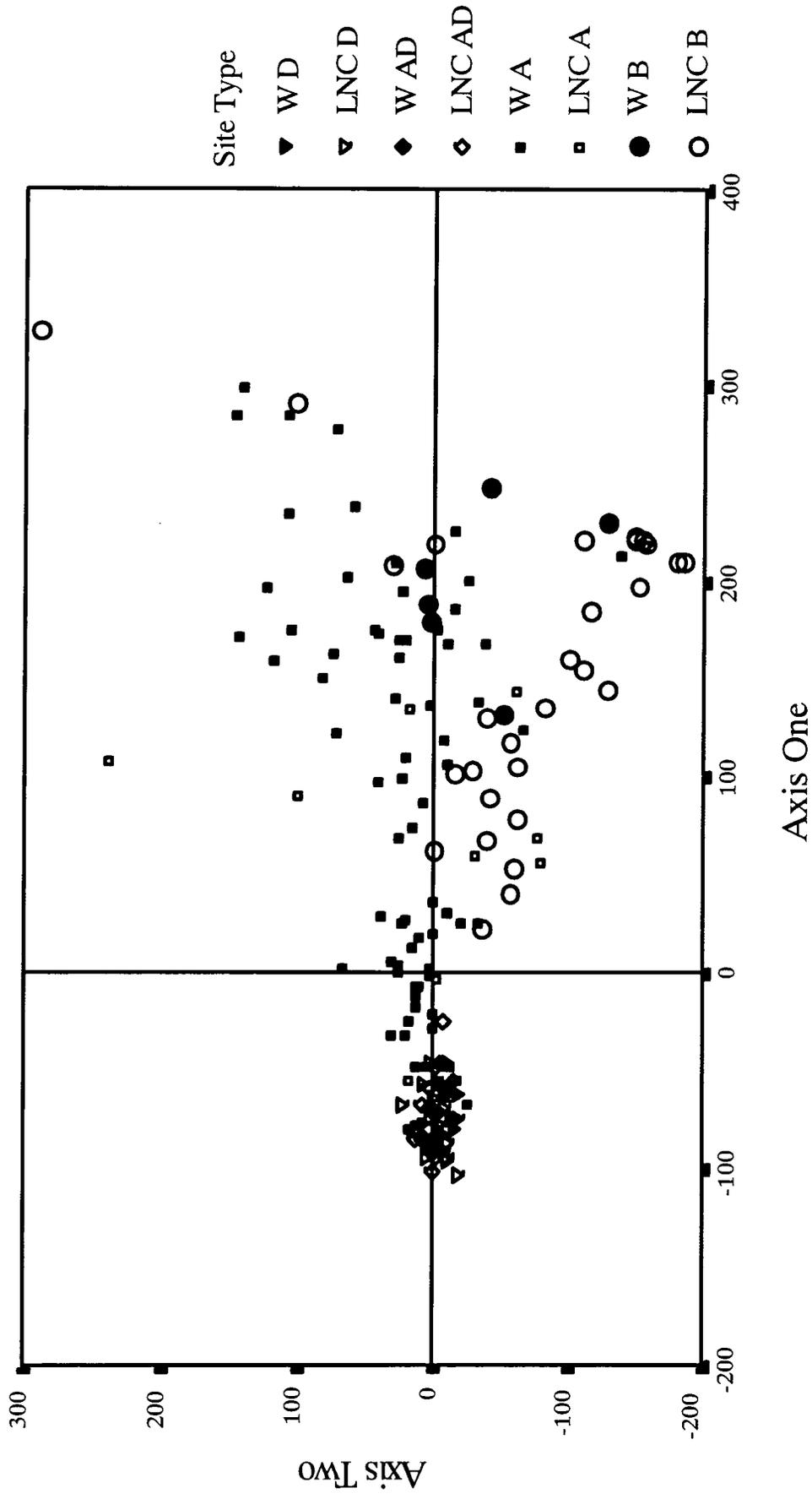


Figure 6: DCA ordination of pools

rarely (e.g. *Hydrachnellae*, *Notonectidae*, *Lumbricidae*). Others, notably *Dytiscidae*, are families which were found in a wide variety of pool types. The ecological tolerances of the families along the second principal axis appear less clear cut than along the first, and it is possible that environmental factors other than those measured contribute to much of the variation exhibited in this ordination.

The ordination of pools on the basis of invertebrates is shown in Figure 6. In this plot, samples (pools) are shown by both site and pool type to allow a greater degree of interpretation of the results. The results of this ordination show a clear clustering of the deeper pool types D and AD. For both the Woodcock Hill sites and those on Loch-nan Clar, the D and AD pools have been placed close together, indicating a high degree of similarity, with respect to their invertebrate fauna, between the two pool types of both areas. This cluster is on the negative side of the first principal axis, in a similar position to the invertebrate groups thought to be indicative of deeper water conditions shown in the ordination of families (Figure 5). There is little spread of the pool samples in this cluster along the second principal axis, suggesting that invertebrate groups found in D and AD pools are responding to only a limited range of variables.

Both A and B type pools exhibit a higher degree of variability, along both the first and second principal axes. There is more variation in pool types A and B along the second principal axis than was shown by types D and AD. There appears to be some divergence between the A and B pool types, with the majority (68%) of A type pools lying on the positive side of the second principal axis, and the majority of Bs (79%) lying on the negative side.

There is no clear grouping together of A and B pool types on a site basis, perhaps due to the variation which exists, especially in the A pools. The majority of the Woodcock Hill site consists of A type pools. Several of the Woodcock Hill A type pools are found within the cluster of D and AD pools. This may result from the fact that larger, deeper A pools are often found on that site.

3. 2. 3 Canonical correspondence analysis

The four environmental variables of depth, edge, pH and temperature were included in analysis of the invertebrate data using CANONICAL CORRESPONDENCE analysis (CANOCO) (Ter Braak, 1987). Again, a log transformation of the data was performed and rare

species were downweighted. Samples 10 and 11 (with no invertebrates) were once more excluded. The eigenvalues for the four principal axes are shown in Table 9. It can be seen that the value for axis one is almost ten times that of axis two, and the values for the second and third axes are very low. In subsequent environmental biplots of the species and sample scores, only the values for axis one and axis two were used. Biplots involving values for the second and third axes were not used as the eigenvalues were so low. Ter Braak (1987) suggests that all ordination axes with eigenvalues below 0.02 should be discarded.

Ordination axis	Eigenvalue
1	0.31697
2	0.03464
3	0.01690
4	0.00743

Table 9: Eigenvalues for the first four principal axes extracted by CANOCO.

Axis one accounted for 84.3% of the variance in the species-environment biplot. Axis two accounted for only a further 9.2%. The third and fourth axes therefore explain only a very small proportion of the variance. With only four recorded environmental variables, it is likely that other, unexamined factors are responsible for some of the variance. The variance inflation factors for the four environmental variables range from 1.4 to 2.1. If a variable was almost perfectly correlated with the other variables, an inflation factor >20 would result, and further interpretation would not be carried out (Ter Braak, 1987). In this case, none of the inflation factors are large, indicating no perfect correlations between the variables.

It should be noted that the axes in the CCA appear to have been 'flipped' when compared with the DECORANA plot of families. The families associated with deeper conditions lie on the negative side of the first principal axis in the DCA plot, and on the positive side of the first principal axis in the CCA plot.

Variable	Canonical coefficients		T-values of regression coefficients	
	Axis one	Axis two	Axis one	Axis two
Pool edge	0.08	0.009	1.9	-0.5
Pool depth	0.562	-0.073	11.1	-3.1
pH	0.138	0.13	2.5	5.1
Temperature	0.093	0.106	-2.0	5.0

Table 10: Canonical coefficients and t-values for first and second axes extracted by CCA.

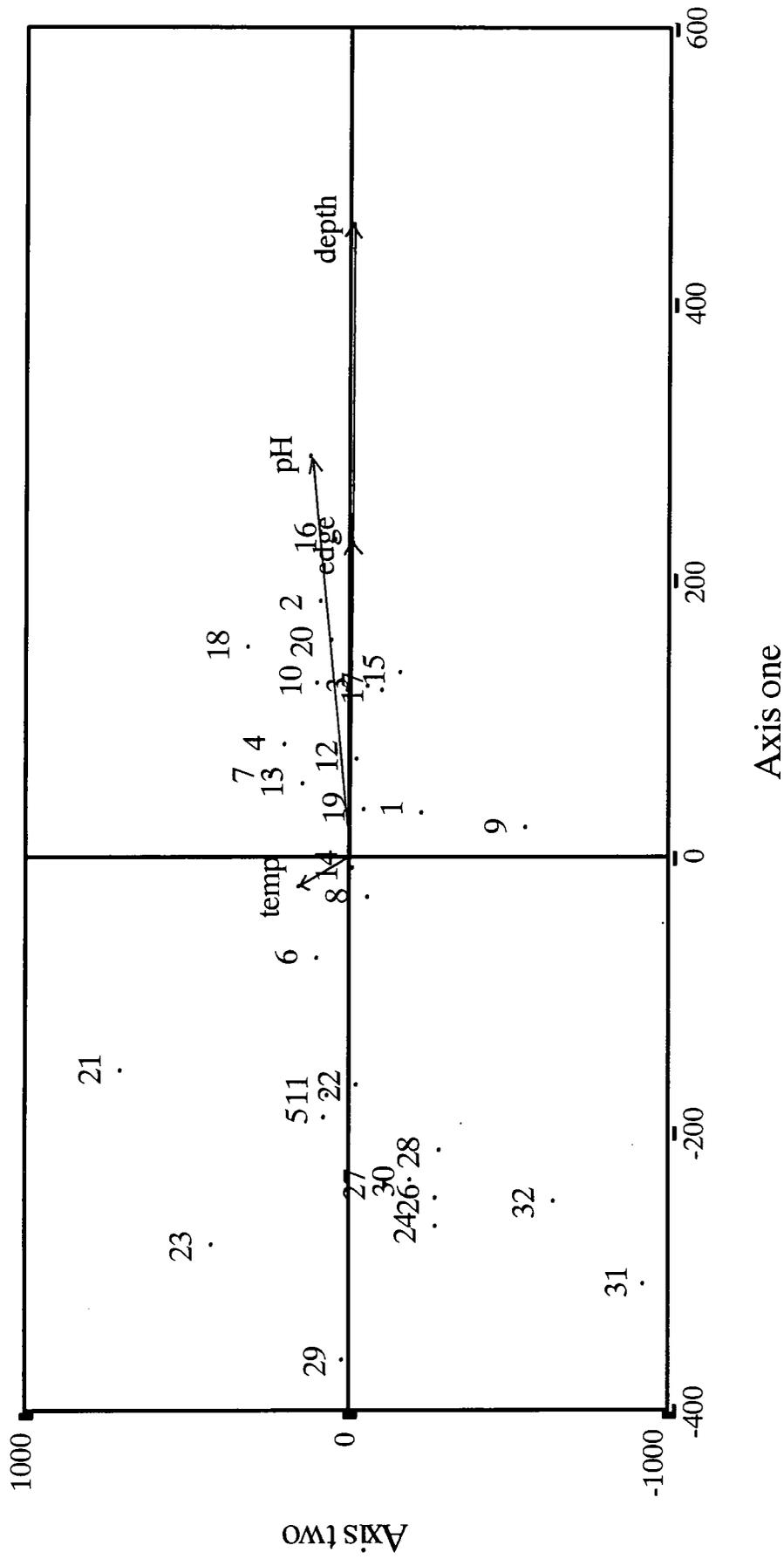


Figure 7: CCA species-environment biplot

Arrows represent environmental variables, times ten.

The canonical coefficients and t-values of regression coefficients for the four environmental variables are shown in Table 10. The larger the canonical coefficient value, the more important that variable is in explaining the variation on that axis. From Table 10 it can be seen that pool depth is by far the most important variable on axis one. The next most important variable on this axis is pH. Pool edge is relatively unimportant on both axes. For axis two, pH and temperature are the most important variables. The t-values indicate that for axis one, depth and pH are significant to the regression, as both of these values exceed the critical value for a t-test at the 5% significance level (1.960, 181df). For axis two, t-values for depth, pH and temperature are all sufficiently high to indicate a significant contribution to the regression. The t-values for edge do not exceed the critical values at the 5% significance level on either axis one or two.

An environmental biplot was produced from the invertebrate family scores and is shown in Figure 7. This shows the environmental variables acting on the families and arrows give an indication of the direction and relative strength of the variables.

The species-environment biplot in Figure 7 shows a group of families on the positive side of axis one which are influenced by a combination of pool depth, edge and pH. The signs of the points in this biplot seem to have been reversed when compared with the plot from the DCA, with group of families occupying the negative side of axis one in the DCA plot occupying the positive side in the CCA biplot. The most important of these variables is depth, indicated by the length of the arrow. Families which are shown to be most affected by these variables include all recorded amphibian species and the families *Gyrinidae*, *Libellulidae*, *Coenagriidae*, *Phryganeidae*, *Sialidae* and *Corixidae*. These are species which in this study were generally associated with deeper pools.

The variables which act on these families appear to have no effect on the families found on the negative side of axis one. This group includes many of the families which were recorded rarely and also *Dytiscidae*, which was a family occurring in a wide variety of pools. There are no corresponding environmental variables for this group of families. If more environmental variables had been included, the main forces acting on this group might have been discovered. Temperature is a variable which appears to have very little influence on any of the families occurring in this biplot.

Following the analysis of the data using CANOCO, a Monte Carlo test was performed with 99 random permutations. This was done in order to test the significance of the environmental variables on the variation in the samples. The environmental variables

acting on axis one were found to have a significant effect ($P < 0.01$) on the variation in the samples on that axis. The four axes taken together did not have a significant effect ($P < 0.07$) on the variation in the samples. This is to be expected given the very low eigenvalues for the third and fourth axes.

3.3 Newts

The numbers and site locations of all newts caught in the two survey periods are shown in Table 11. The most striking difference between the two surveys concerns the total number of newts caught. In the second survey there was a 44% reduction in the number of larval newts caught overall in survey one, as well as large reductions in the numbers of adult male and female palmates. The number of adult palmate newts caught was low in both surveys.

Site	Survey one			Survey two		
	Adult male	Adult female	Larvae	Adult male	Adult female	Larvae
LNC I	3	1	31	3	0	28
LNC II	2	1	27	0	1	10
W I	4	4	18	2	0	7
W II	4	3	42	1	1	21
Total	13	9	118	6	2	66

Table 11: Numbers and locations of newts caught during surveys one and two.

3.3.1 Newt location and habitat utilisation

Pool edge and depth

For each pool in which a newt (adult, larvae or tadpole) was caught during survey one and survey two, details of the pool type, amount of edge and water depth were compiled. The mean pool depth and edge was calculated for all pools in which newts were found during the surveys, on a transect by transect basis. The mean depth and edge for all pools on each transect were then calculated and the results can be found in Appendix 4. A summary of the results by site for survey one is shown in Table 12.

Site	Mean depth all pools with newts	Mean depth all pools (cm)	Mean edge all pools with newts	Mean edge all pools (m)
LNC I	31.58	15.60	79.33	34.76
LNC II	25.34	17.63	60.25	41.95
W I	25.13	16.20	65.60	39.44
W II	21.00	12.95	78.50	43.29

Table 12: Mean depths and edges of pools containing newts, survey one.

Site	Mean depth all pools with newts	Mean depth all pools (cm)	Mean edge all pools with newts	Mean edge all pools (m)
LNC I	33.33	15.60	69.17	34.76
LNC II	25.63	17.63	65.56	41.95
W I	23.75	16.20	71.92	39.44
W II	18.33	12.95	58.44	43.29

Table 13: Mean depths and edges of pools containing newts, survey two.

From Tables 12 and 13 it can be seen that the mean depth and size (in terms of the amount of edge) of pools which contained newts is up to twice that of the mean for pools on the site as a whole. The implications of this are that larger, deeper pools are being utilised to a greater extent than smaller, shallower pools.

Pool type

For survey one, the number of each pool type available on each site (Table 2) was related to the number of pools of that type utilised (indicated by presence of newts at the time of survey). This gave some indication of the use of each pool type with respect to its availability. The data from the first survey was used as it provided more information in terms of the number of pools found to contain newts. A table containing the detailed information for this can be found in Appendix 5. In summary, on the Loch-nan Clar sites, 79.9% of AD pools were found to contain newts, and 75% of D pools. On the Woodcock Hill sites, 60% of both AD and D pools were utilised. The percentage of A pools utilised was much lower, with 11.8% and 22.8% for LNC and W respectively.

No B pools on either Loch-nan Clar or Woodcock Hill were found to contain newts in either survey.

3.3.2 Newt abundance

In order to assess the relative abundance of adult and larval newts on the four sites, an estimate of newts caught per unit time was made. For each site, the total number of newts caught in each pool type was determined, followed by the total time spent sampling in each pool type (Appendix 6). These figures were then used to calculate catching rates (newts caught divided by time spent surveying). Table 14 shows the catch rates per minute for both surveys.

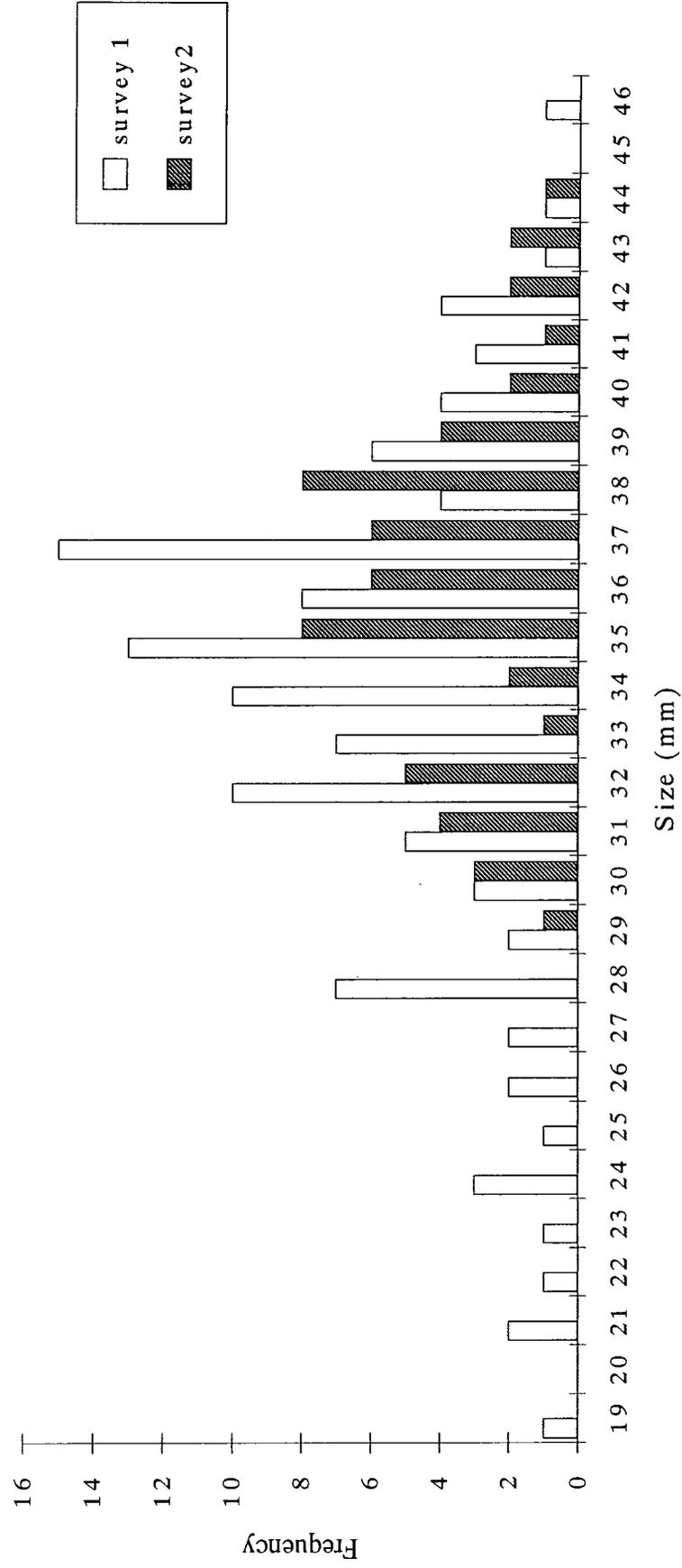
Survey one					Survey two			
Site	B	D	A	AD	B	D	A	AD
LNC I	0.0	0.073	0.0	0.109	0.0	0.028	0.0	0.031
LNC II	0.0	0.095	0.096	0.272	0.0	0.052	0.038	0.109
W I	0.0	0.052	0.148	0.033	0.0	0.052	0.123	0.029
W II	-	-	0.040	-	-	-	0.015	-

Table 14: Catching rates per minute, by pool type for surveys one and two.

The catching rates were almost all lower in the second survey than in the first. The catching rates at W I fell the least, with the value for D pools remaining the same. In the first survey, the catching rate was higher in D pools on LNC than on W (0.08 compared with 0.05), but A pools on Woodcock Hill were, on average, higher than on Loch-nan Clar (0.09 compared with 0.05). Catching rates in AD pools on LNC were the highest found in survey one (0.19), though the rate on W was much lower (0.03). In survey two, the catching rate in woodland A pools (0.07) was higher than in D pools (0.03) on Loch-nan Clar, although this was matched by AD pools on that site. Overall, the catching rate on Loch-nan Clar in survey one was higher than that on Woodcock Hill (0.107 compared with 0.057), but in the second survey, LNC had a slightly lower rate than W (0.043 compared with 0.05). Over both surveys, more newts were caught per minute on Loch-nan Clar (0.076 compared with 0.053 on Woodcock Hill).

In order to assess differences in catching rates between the four sites, use was made of Kruskal-Wallis one-way analysis of variance, correcting for ties. Firstly, a test was made to ensure that the amount of time spent on each site was comparable. Secondly, differences in the number of newts caught on each site were tested, and lastly, newts caught per minute on each site. In all cases, the sites were treated as equal, differing only in location, and the null hypothesis was that the population medians (catching rates) would also be identical. In the case of time spent surveying on each site, this hypothesis was accepted (Chi-square = 6.406, 3df, P<0.05).

Figure 8: Larval newt size frequency distribution, Surveys one and two.



For both the numbers of newts caught and catching rates, the null hypothesis had to be rejected (Chi-square = 8.948, 3df, $P < 0.030$; and 10.735, 3df, $P < 0.132$ respectively) illustrating that differences in these factors occur between the sites.

3.3.3 Newt sizes

Larvae

The size of the 118 larvae caught in survey one ranged from 19 to 46 mm. These values are for total length; from the tip of the snout to the end of the tail. In the second survey, the 66 larvae ranged from 29 to 44 mm. The values for the means and standard deviations of the larval sizes are given in Table 15. These show that there is less variation in size in the second survey, and that the mean size is also larger than in the first survey. All newt size data is in Appendix 7.

Survey one				Survey two			
n	Mean	SD	Range	n	Mean	SD	Range
118	33.92	5.20	19-46	66	36.03	3.43	29-44

Table 15: Total lengths for larvae, surveys one and two.

Figure 8 shows the frequency of larval sizes for surveys one and two. One thing which seemed to stand out from the examination of this histogram was the absence of all newts up to 28 mm in length, and the lower numbers, especially of larger individuals, found in the second survey. The interpretation of this will be dealt with in the discussion. It is clear from these figures that the majority of larvae in the first survey fell into the 30 - 40 mm range, with few individuals falling into the smallest and largest size categories. The individuals in the second survey also followed this pattern, and both sets of data were found not to differ significantly from the normal distribution using a Kolmogorov - Smirnov test. This was taken as justification for later application of parametric statistical tests. A t-test applied to the data from the first and second surveys yielded a significant difference between the two means (t-value = -2.95, 182df, $P < 0.004$). A t-test was also applied to test for differences in larval sizes between Loch-nan Clar and Woodcock Hill. For both surveys there proved to be no significant difference between the mean sizes on the two sites (survey one: t-value = 0.26, 116df, $P > 0.05$; survey two: t-value = -1.18, 64df, $P > 0.05$).

Adults

Few adults of *Triturus helveticus* were caught in either survey. Again the pattern found with larvae was repeated here, with 22 individuals captured in the first survey and only 8 in the second. More males than females were caught in both surveys, 13 males and nine females in survey one, and six males and two females in survey two. The sizes recorded for the adults in both surveys was not found to differ significantly from the normal distribution (Kolmogorov - Smirnov goodness of fit test). Table 16 shows the mean sizes and size ranges for adult newts caught in survey one.

Adult male				Adult female			
n	Mean	SD	Range	n	Mean	SD	Range
13	66.7	3.0	62-71	9	72.9	3.0	68-79

Table 16: Total lengths for adult newts, survey one.

The mean lengths of adult males and females fit fairly well with those found by Harrison, Gittins and Slater (1984), who recorded an average male length (excluding tail filament) of 66.8 mm, and for female palmate newts, an average of 76.5 mm. The small sample size for the latter may be responsible for the smaller mean female size, as individuals up to 79 mm were found, and in the second survey, only two females were caught, measuring 76 and 77 mm.

The tail : body ratio ranged from 0.77 to 0.89 in male palmates, and from 0.66 to 1.03 in females (survey one). The median values are 0.85 and 0.89 for males and females respectively. All newts but one in the first survey had tails which were shorter than the combined length of the head and body. This finding concurs with that of Harrison, *et al* (1984) and Bell (1966). Other studies have found the reverse to be true, but Harrison *et al* (1984) suggest that discrepancies in measuring techniques may have contributed to this.

4. 0 DISCUSSION

4. 1 Habitat utilisation by *Triturus helveticus* during the aquatic phase

Water chemistry, pH, depth, presence of predators, availability of food and suitable egg laying substrate are all factors which may influence the suitability of a breeding pool to a given newt species.

Vegetation in a pool may be an important factor; if not in the actual choice of pool for breeding, then in the survival of newts. Aquatic vegetation provides cover for both adult and larval newts as well as a substrate for egg laying. Cooke and Frazer (1976) found that all three newt species in Britain tended to breed in ponds having an abundance of aquatic vegetation. Investigations of aquatic habitat selection in the Netherlands by Strijbosch (1979) showed that newts tended to avoid open water when spawning; thus, pools with aquatic vegetation are more suitable than pools lacking vegetation.

Strijbosch (1979) suggests that newts are less dependent on water depth due to the attachment of eggs to vegetation structures. The presence of *Menyanthes trifoliata* in D pools does not provide cover for adults or eggs, as the leaves tend to be raised above the surface of the water, with only a bare stem submerged.

Analysis of the proportions of each pool type utilised by *T. helveticus* in this study reveals a preference for AD and D pools on both Loch-nan Clar and Woodcock Hill. This is surprising as D pools appear to be less suitable breeding sites than A or AD pools, due to the characteristic lack of submerged vegetation (see Methods 2.2). However, these D and AD pool types are generally larger than A and B pools, and are less prone to desiccation during periods of drought, so in the Flows these can be viewed as providing a more stable breeding habitat, than vegetated but shallow pools.

B pools are totally unsuited as newt breeding pools. These shallow pools often lack vegetation and are also liable to desiccation.

The A type pools on Loch-nan Clar appear to be similarly unsuitable as breeding pools. On Woodcock Hill, A pools tend to be deeper (Table 3) and on W II in particular there are many large deep A pools. The absence of all other pool types here and the presence of newts illustrates the ability of *T. helveticus* to utilise whatever habitat is available.

The preference for D and AD pools on the other sites is also related to the different character of the A pools on those sites. The deeper A pools present on W II can be viewed as a kind of surrogate D pool. These large A pools may be more favourable than D pools on other sites as they are often large, deep and have much aquatic vegetation.

The pool complexes which are characteristic of much of the Flow country provide ideal habitat for *Triturus helveticus* during the aquatic phase because the large number of pools present on the complexes means that the probability of the presence of suitable pools is higher in comparison with scattered pools in a landscape. Further, the greater the number of pools in a given area, the more stable the population, with reduced risk of extinction due to any one pool drying up or being predated out. If catastrophic mortality occurs in one pool, there is the possibility of repopulation from an adjacent pool (Mann, Dorn and Brandl, 1991). In complexes such as those on Loch-nan Clar and Woodcock Hill, the long term population stability may be increased, as the probability that *T. helveticus* will be present somewhere in the whole group of pools increases, allowing repopulation of pools. Mann, Dorn and Brandl (1991) suggest that catastrophic mortality within amphibian larvae is common.

4. 2 *Triturus helveticus* in the terrestrial phase

Dodd and Callan (1955) and van de Bund (1968) state that adult palmate newts migrate to water in the Autumn and hibernate in the water. This pattern was also found by van Gelder (1973), who noted that the majority of adults migrate to water in the Autumn, whereas few hibernate on land and migrate to water in the Spring. Other authors (Mertens (1947), Smith (1951), Dolmen (1981), and Harrison, Gittins and Slater (1983)) have observed palmate newts (smooth newts in the case of Dolmen (1981)) hibernating on land.

Frazer (1983) states that newts hibernate under stones, in cracks in the ground and even in long grass, and that *T. helveticus* has the general newt pattern of emergence from refugia and movement to the breeding sites in March/April. Harrison *et al* (1983) found the main in-migrating period for palmates at a pond in mid-Wales to be early February to mid-April. Migration from the water at the end of the breeding season occurred mainly between 25 May and 23 July.

In the present study sites, suitable terrestrial habitat for overwintering adults is unlikely to be of the types mentioned in the literature. No stones or wood are present on the surface of the bog and there are no long grasses which would provide effective protection from freezing. The weak limbs of *T. helveticus* are unsuitable for digging, so only natural shelters or burrows made by other animals are utilised (Frazer, 1983). Wet ground has to be avoided during hibernation, so cracks in the waterlogged peat present on the sites in this study would not provide suitable refugia. There is also the possibility of freezing while hibernating in such cracks. One possibility for overwintering refugia are the *Racomitrium lanuginosum* hummocks which were often seen to have burrows (including abandoned otter holts) present.

Once larvae metamorphose, they migrate out of the pools and remain on land for at least two years, until sexually mature. No metamorphosed juveniles were caught in pools on either survey, suggesting that at metamorphosis, newts begin the terrestrial phase. If juveniles are able to overwinter on land, it seems likely that adult newts are also able to do so. Figure 9 represents a summary of the life cycle of *T. helveticus* in the Flow Country, based on available data.

The alternative is that post-metamorphic juveniles spend a brief period on land before returning to the pools in Autumn for hibernation. If hibernation occurs in the water, there is a risk of mortality due to freezing of the pools. Griffiths (1984) observed no overwintering in pools by adult palmates and suggests that due to varying degrees of freezing and drying between September and February, it seemed unlikely that overwintering newts would have survived. Griffiths (1984) suggests that overwintering adults might only occur in large pools. Large D or AD pools might be buffered against water level changes and extremes of temperature.

Further work is needed here to establish the details of the overwintering of *T. helveticus* in the Flow country.

4.3 Migration to water

It is likely that the urge to seek water for breeding is under hormonal control, but the numbers of newts active on a given night during the inward migration period is influenced by environmental factors; principally temperature and rainfall/humidity (Harrison *et al*, 1983). Inward migrations of newts observed by Harrison *et al* (1983) in mid-Wales were

interrupted by a period of cold , frosty conditions, and it is suggested that there is a minimum temperature above which newts can become active.

Newts are susceptible to desiccation by evaporative losses through the skin and so emerge from refugia when levels of humidity are adequate. Smith (1973) suggests that movement occurs mainly on wet nights. Humidity and temperature are thus both important factors influencing the activity of newts during inward migrations.

The timing of the breeding migrations of adult *Triturus helveticus* (assuming overwintering on land) in the Flow Country, as elsewhere, is likely to be affected by environmental conditions. Meteorological data was collected at Loch-nan Clar and is contained in Appendix 8. The rainfall data was collected between 4 May and 31 July, and maximum and minimum temperatures were recorded from 19 May to 31 July. From the rainfall data it can be seen that there was a period of about three weeks, from the start of May, with very little rainfall. It is possible that this dry period could have interrupted the breeding migration of the newts, as activity is reduced in dry conditions.

4. 4 Egg laying and the timing of breeding

Frazer (1983) states that in the palmate newt, eggs are laid individually, on aquatic vegetation , and this starts in early April. He also suggests that an average female palmate may be capable of laying 350 eggs or more in a Summer. In this study, no eggs or young newt larvae were recorded until the second survey at the end of June. In this survey, only one egg was recorded in a total of 100 pools searched. Very few pools with the current years larvae were recorded; only nine pools, compared with 50 pools with juveniles in survey one and 35 in survey two. Eggs are usually well concealed but tadpoles are very obvious when caught, and so would certainly have been noticed if present in the first survey.

The absence of newt eggs and tadpoles at the time of the first survey suggests that egg laying at least had not begun at this time. This may be accounted for in several ways. The apparent late start to the breeding season may be linked to the very dry period in May which may have delayed breeding by interrupting the migration of adult newts to the water. This dry period may also have caused some direct mortality of newts both in refugia and during migration itself due to evaporative losses from the skin.

If the density of adult newts is low and there are large numbers of pools in an area, this may reduce the encounter rate between the sexes to the point where breeding success is affected. Griffiths (1984) found that although some inter-pond movement occurred, most palmate newts tended to remain in one or two pools during the breeding season. This is not necessarily the case in the pool complexes in this study, where pools are very close together, but it remains unknown to what degree newts sample several pools before settling in one.

Another possibility is that breeding in this area does not normally start until July and that the year of this study is a normal one, unaffected by the environmental conditions in May. It is obvious that further work over a number of years is required to build up an adequate picture of the timing and behaviour of breeding in *Triturus helveticus* in the Flow Country, but the best estimates from present data indicate that breeding starts in late June and July.

4. 5 Predation of eggs and larvae

Like all amphibians newts have high fecundity but low larval survival, suggesting a significant role for predation and interspecific competition during the larval stages (Griffiths, de Wijer and May, 1994). Eggs are usually wrapped or enclosed on leaves by the female, with the egg membrane acting as an adhesive to maintain the folds (Miaud, 1993). Smith (1973) states that occasionally newts lay eggs in pools devoid of vegetation. In these cases eggs are found attached to dead leaves or pieces of wood with no apparent attempt at concealment.

Egg survival in *Triturus* spp. is assumed to vary between years and between breeding sites, but has been shown to be very low by several studies. Bell and Lawton (1975) found a 3% hatching rate among *T. helveticus*, and Miaud (1993) a higher rate of 16%. Miaud (1993) suggests causes of low egg survival include intrinsic embryonic mortality, environmental disturbance (pollution, drying), and predation. Miaud (1993) studied the predation of *Triturus alpestris* eggs under pond and aquaria conditions. Survival of eggs was found to be significantly higher when eggs were enclosed in plastic netting, suggesting predation as the major mortality risk.

In experimental situations, Miaud found that *T. alpestris* eggs were consumed by Dytiscids (*Dytiscus marginalis* and *Acilius sulcatus*). Adults and larvae of *Dytiscidae*, *Hygrobiidae*, *Hemiptera* and *Libellulidae* are known to predate numerous aquatic animals

including fish and amphibians (Miaud, 1993). Adults of *T. helveticus* and *T. alpestris* also fed on eggs in these experiments, and such intraspecific oophagy has been observed to be sex specific, with females consuming most eggs (Marshall, Doyle and Kaplan, 1990, Miaud, 1993). The wrapping of eggs by females has been shown by Miaud (1993) to decrease mortality, except in the case of *D. marginalis*, which ate wrapped and unwrapped eggs in equal proportions. Wrapping of eggs in vegetation is thought to increase the survival of eggs by making them less visible and accessible to predators.

The implications of these studies of predation of newt eggs are that in pools where little aquatic vegetation is available as an egg laying substrate, mortality is likely to be greater than in pools where there is an abundance of vegetation. Thus D pools would again appear to be less favourable for newts in terms of egg survival.

The very high mortality rate in newt eggs is offset by high fecundity and the relatively long lifespans of newts; *T. helveticus* is thought to live for up to ten years in the wild.

4. 6 Development rates and pH

The implications of low pH on the abundance and development of amphibians are of importance in relation to this study. Under conditions of low pH, embryonic mortality and delayed or deformed hatchlings may occur (Griffiths, de Wijer and Brady, 1993). Griffiths *et al* (1993) also point out that tolerance to acidity increases with the development from embryo to adult (with the latter probably being more resistant to conditions which would kill earlier stages).

Reductions in growth and survival have been documented in amphibian larvae as a result of acid conditions (e.g. Warner, Dunson and Travis, 1991, Griffiths *et al*, 1993). Cooke and Frazer (1976) report that *T. helveticus* can tolerate pools with a pH as low as 4.0. When comparing the development and growth of *T. helveticus* and *T. vulgaris* larvae under neutral (pH 7.4) and sublethal acid (pH 4.45) conditions, Griffiths *et al* found that survival to hatching was reduced in both species under low pH. The low pH used in these experiments was higher than that recorded in any of the pools in this study (range: 3.99-4.43). It therefore seems likely that *T. helveticus* is at the lower end of its pH range in the Flow Country. The temperature used in these experiments ranged from 17-24°C, which again is higher than that encountered in the pools during this study.

Under the acid conditions in the experiments of Griffiths *et al* (1993) *T. helveticus* hatched at an earlier stage and at a smaller size than under neutral conditions and larval growth rate was also reduced. Griffiths *et al* (1993) suggest the effects of pH are consistent with the general low abundance of both *T. helveticus* and *T. vulgaris* in acidic pools (e.g. Cooke and Frazer, 1976). This would also appear consistent with the relatively low abundance recorded in this study. Earlier hatching in acid water could expose larvae to predation for longer (Griffiths *et al*, 1993) and combined with the reduced development rate, this could have significant effects on survivorship in larvae. Henrikson (1990) points out that most predators prefer small tadpoles. With increasing age and size, the handling time required to deal with the prey may also increase. Henrikson (1990) also states that there is evidence for maximum predation pressure when amphibians are young. Under the conditions of low pH and temperatures prevalent in the pools in this study, it is possible that the resulting slower development contributes to higher larval mortality than would otherwise occur.

Newt larvae feed on live prey and low pH has been shown to cause depressed feeding behaviour, and food resources themselves may be limited by acid conditions (Griffiths *et al*, 1993, Griffiths, 1993). The effects of pH on feeding behaviour in *T. helveticus* have been studied by Griffiths (1993), again under neutral and sublethal acid conditions. *T. helveticus* exhibited suppressed feeding behaviour under acid conditions (pH 4.45). Palmate larvae approached and orientated towards food but snapping was inhibited. Suppressed feeding behaviour is another factor which may contribute to the slower development of *T. helveticus* under acid conditions. Griffiths (1993) suggests that conditions of low pH interfere with the chemosensory system, since the orientation and approach towards food indicates visual and tactile systems are unimpaired. It is apparent that complex interactions are in operation with respect to pH, mortality and development rates, and further study is needed in this area.

4.7 Metamorphosis and larval size

The results of this study indicate a complex picture of metamorphosis and migration in *T. helveticus*. According to the literature, eggs take around two weeks to hatch. Larvae normally take around three months to reach the stage of metamorphosis, after which they leave the water to begin a period of land habitation (anything up to seven years) until sexually mature. The first amphibian survey in this study was carried out in late May, during which a total of 118 larvae were caught, with an average length of 33.9mm.

Larvae were also captured on Loch-nan Clar in mid-April. Because of their size, it was concluded that these larvae must have been the product of the previous years breeding which had subsequently overwintered in the pools. The alternative was that these were the result of very early breeding in the year of capture, which would have meant that breeding took place in February/March. This was considered to be very unlikely due to the environmental conditions of low temperature prevailing at this time. Also if breeding had begun early in the year, i.e. February, it had also ceased early, with no continuation. Tadpoles obviously of the current year were not found until July.

It seems likely, therefore, that breeding in the Flows occurs in June/July and a proportion (not necessarily all) of that years larvae hibernate in the pools and metamorphose the following Summer. It is possible that some larvae reach metamorphosis in their first year, although this depends on the date of breeding and the rate of development; neither of which are known in this case.

Studies by van Gelder (1973) in the Netherlands showed that a proportion of the larval population of *T. helveticus* hibernated in the water. Immature juveniles (post-metamorphic) were caught in two periods; June/July, and a smaller group in August-October. This pattern was displayed through all three years of the study. The later emergent newts were taken to be from that years breeding, and the earlier group were the juveniles which had overwintered as larvae.

Further evidence supporting the hypothesis regarding overwintering juveniles in the Flows came from the sizes of the larvae caught in the two surveys and comparisons of these with the sizes of post-metamorphic larvae in published work, and also from metamorphosed larvae caught in terrestrial pitfall traps on Loch-nan Clar and a nearby site at Badanloch. This data covers the period from 3 May to 11 August 1994. Pitfalls were collected on a fortnightly basis, and no juvenile newts were caught until 30 June. A total of 29 juveniles were caught in the trapping period, the majority (93%) on Badanloch.

	n	Mean	SD	Range
Pitfall data	29	39.28	2.53	35-44
Survey one	118	33.92	5.20	19-46
Survey two	66	36.03	3.43	29-44

Table 17: Sizes of metamorphosed (Pitfall data) and aquatic larvae (all sizes in millimetres)

The data in Table 17 shows that some of the larvae caught in both survey one and two were within the size range shown by metamorphosed larvae caught in pitfalls. The interpretation of this data and that shown in Figure 9 is that the larvae grow through the year and metamorphose at a certain stage. The larvae caught in survey two were, on average, larger than those in the first survey, and no larvae smaller than 28mm were caught. It seems likely that the smaller individuals in survey one are growing into the larger size category in survey two. The larger size category in the second survey does not show this influx of larvae because metamorphosis and migration of newts of this size is occurring at the same time, as shown by the data from the terrestrial pitfall traps. However, it is also possible that the reduction in numbers of larvae caught in the second survey is a result of predation.

As well as hibernating in the pools and metamorphosing the following year, it is possible that some larvae are able to reach metamorphosis in their first year, although later than the previous years larvae. Therefore, if the majority of second year juveniles are caught in late June -August, the metamorphosed first year larvae would be represented by smaller individuals caught on land at a later date, perhaps September-October. First year juveniles would almost certainly be smaller than second year juveniles as a result of the shorter period of development. Sizes of juvenile *T. helveticus* at metamorphosis are given as 29-35mm by van de Bund (1968) and 25-30mm by Smith (1973). In the Netherlands, van Gelder (1973) found that although the majority of larvae metamorphosed in August and September, a small proportion regularly overwintered and metamorphosed as larger individuals the following year. Van Gelder (1973) also found that the size of first year larvae was much less than that of second year larvae (Means of 33.6mm and 38.6mm, respectively). The length of larvae at metamorphosis increases as the season progresses. Further study is necessary to determine whether or not any larvae metamorphose in their first year in the Flow Country, and, if so the proportion of the larval population which overwinters in the water.

4. 8 Absence of other newt species

If a species is not seen or caught at a site, this does not necessarily mean that the species is absent, although Cooke and Frazer (1976) suggest that a second netting usually produces the same result. In the present study, failure to record other newt species was taken to imply absence, although one can never be certain. Although the larvae of *T. helveticus* and *T. vulgaris* are indistinguishable by external morphology (Giffiths, de Wijer and May,

1994), the fact that no adult *T. vulgaris* were found, and were unlikely to be present led to the assumption that all larvae were those of the palmate newt. Griffiths (1986) states that smooth newts (*Triturus vulgaris* (L.) and palmates are frequently observed coexisting in Britain. The two species are of a similar size, general morphology and behaviour, and many pools are suitable for both species.

Triturus vulgaris and *T. helveticus* display some tendency to be ecologically separated according to water chemistry (Cooke and Frazer, 1976), with some degree of overlap. At the extremes of conditions most favourable to one species, the other tends not to be found. The warty (or great crested) newt, *T. cristatus* and the smooth newt were found to be less common in pools of pH <6.0 by Cooke and Frazer (1976), Beebee (1983) and Denton (1991). Smooth and warty newts were found to occur mainly in ponds with a pH >7.0 by Yalden (1986), whereas palmates were found in pools of pH <7.0. Dolmen (1980) found smooth newts in Norway in pools below pH 6.0 (down to pH 4.5) but Cooke and Frazer (1976) suggest that smooth newts may not be able to survive and breed normally below pH 6.0. Palmates are found regularly down to pH 3.9. The low pH of pools in the present study may explain the absence of *T. cristatus* and *T. vulgaris*, although Griffiths (1993) found that low pH did not suppress feeding behaviour in *T. cristatus* as it did in *T. helveticus* and *T. vulgaris*. This raises questions concerning the apparent greater tolerance for acid conditions associated with *T. helveticus*, and the absence of *T. cristatus* from such waters.

Smooth newts tend to be found in water with relatively high concentrations of metals and palmates appear to prefer metal deficient water. Studies by Denton (1991) in Cumbria found that *T. vulgaris* can survive in pools where either calcium or potassium, or both, are present in high concentrations, whereas *T. helveticus* can breed in ponds deficient in both metals, and rarely occurs where calcium levels exceed 20mg/l. Cooke and Frazer (1976) state that *T. cristatus* is rarely found in the absence of *T. vulgaris*, and the two species have almost identical distributions in Britain. *T. cristatus* and *T. vulgaris* are relatively less common in soft water areas, and *T. helveticus* is less common in hard water areas.

It seems unlikely that *T. cristatus* or *T. vulgaris* populations exist in the pool complexes on Loch-nan Clar or Woodcock Hill as the conditions are likely to be at the extremes of these species tolerances.

4.9 Associations of invertebrate families

In the DECORANA ordination of families (see Figure 6), newt tadpoles, larvae and adults all appear in a cluster, together with *Chaoboridae* (pupae), *Leptophlebiae*, *Libellulidae*, *Coenagriidae*, *Gyrinidae*, *Corixidae*, *Phryganeidae*, *Chironomidae*, *Sialidae* and *Trichoptera*. *Chaoboridae* (pupae) and *Chironomidae* are both likely prey items of *T. helveticus* in the Flow Country. Avery (1968) found that adult *Corixidae* and nymphs of *Odonata* (*Libellulidae* and *Aeshnidae*) were occasionally eaten by *T. helveticus*, though not in proportion to their abundance in the habitat. *Corixidae* and *Libellulidae* are among the invertebrate families which prey on newt eggs and larvae. Other families in the cluster along with *T. helveticus* include *Coenagriidae* and *Sialidae*, again potential predators of *T. helveticus*.

The DECORANA ordination (Figure 6) produced a group containing *T. helveticus* and various invertebrate families. It is possible that all of the families in this group are found together because they respond to the same environmental variables. Another possibility is that *T. helveticus* selects pools where prey items are abundant, and that these are also pools where predators of newt eggs and larvae are found.

The CANOCO species-environment biplot in Figure 8 shows that all four amphibian categories, particularly newt adults and larvae, are associated with greatest pool depth. As pools are used as overwintering habitat by *T. helveticus* larvae, and possibly adults, pool depth is of potentially great importance. Deeper pools may be less prone to freezing during the Winter, and newts would be expected to be found in those pools which are buffered against the extremes of temperature.

4.10 Impacts of afforestation on *T. helveticus*

At the outset of the present study, it was unknown whether populations of *T. helveticus* existed on either of the sites on Woodcock Hill. The presence of pool complexes surrounded by trees raises questions concerning the current and future viability of these sites as newt breeding habitat. That *T. helveticus* survives and breeds on both of the afforested sites in the present study indicates that they are adequate for newts at the current time.

Lindsay *et al* (1988) state that the effects of afforestation of blanket mire on the ecology of associated freshwater systems are profound. They suggest that physical changes such as timing and quantity of runoff have important impacts on freshwater flora and fauna. Eutrophication due to fertiliser treatment and pesticide application are also likely to cause problems in some freshwater systems. However, the afforestation of areas of blanket bog around pool complexes such as those in the present study is likely to be of limited detrimental effect to *T. helveticus* and other amphibians, at least in the short term.

The complexes on Woodcock Hill have not been planted with trees as these areas are too wet. Only areas which can be successfully ploughed and drained will support trees, and it follows that the drier areas are also least likely to be utilised by newts as breeding sites. It is possible that the afforestation of some areas adjacent to pool complexes may actually be of benefit to *T. helveticus*. Although the pool complexes themselves are not planted, afforestation is likely to have an effect on the hydrology of the sites. The water table will be lowered by drainage, and as trees become established, increasing evapo-transpiration rates may lower the water table further. This, however, may be of benefit to newts by improving areas around the complexes in terms of overwintering refugia. A lower water table and deep cracking of peat may provide suitable places for overwintering newts.

The ploughing of the peat surface and creation of drains exposes rocks and buried tree stumps. These, together with the ridges of overturned peat used for planting seedlings above the peat surface, may provide further opportunities for terrestrial overwintering sites. The activities involved in the establishment of trees on blanket bog may thus provide the sorts of cover found naturally in other parts of the country. If *T. helveticus* does overwinter on land in the Flow Country, supplementary terrestrial habitat may improve survivorship. Further study would be needed to reveal whether such refugia are used on Woodcock Hill, and if so, if this leads to any increase in survival among juveniles and adults. The absence of refugia of this type on the complexes on Loch-nan Clar does not prevent the survival of *T. helveticus*, indicating that these refugia are not essential for newt survival.

4.11 Concluding remarks

This study has raised many questions concerning the ecology of *Triturus helveticus* in the Flow Country. Given the importance of this area and the fact that the habitat is unique, the need for further research is self evident. The rate of mortality in eggs and larvae of

newts is high, and the possibility of further predation of larvae during slow development brought about by low pH means that the odds may appear stacked against the survival of *T. helveticus* in this area. In addition there are factors such as the apparent lack of terrestrial refugia and the associated risks of freezing and desiccation, which seem to make the existence of *T. helveticus* in such an environment still more unlikely. Notwithstanding these factors, populations of the palmate newt were found on all four sites chosen for the present study, including a site on Woodcock Hill where only one pool type was present.

The present study represents merely a snapshot of *T. helveticus* in the Flow Country, and as such it is very difficult to determine details of the palmate newt life cycle in this unusual environment. Nevertheless it is clear that the situation may be very different to that encountered elsewhere, as indicated by the presence of overwintered larvae in many pools, and apparent lack of terrestrial refugia.

The pool complexes found in the Flow Country may be viewed as suitable habitat for *T. helveticus* during the aquatic phase. The large number and variety of pools within these complexes makes total extinction on a site unlikely, given the possibility of recolonisation from neighbouring pools. Afforestation of blanket bog adjacent to pool complexes is not likely to be detrimental to *T. helveticus*, although the effects at the closed canopy stage and during harvesting may be more profound.

There is much further work which can, and should be carried out on *T. helveticus* in the Flow Country, given the importance of gaining further understanding of the ecology of this area. Estimates of populations could be carried out using mark and recapture experiments, or by enclosure of individual pools. The present study also raised questions concerning the overwintering habits of juveniles and adults in the Flows. The degree of intrahabitat wandering during the breeding season is also of potential importance given the large numbers of pools on these complexes and the relatively small newt populations generally associated with acidic waters. Other aspects which may be of interest include the timing and length of the breeding season, dietary studies and aquatic microhabitat use. The development rates of larvae and age at first breeding are also of great interest. Further research needs to be carried out into the ecology of *Triturus helveticus* in the Flow Country to establish answers to questions raised by this study, and this will involve many years work in this precious and fragile ecosystem.

5. 0 REFERENCES

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6.0 APPENDICES

APPENDIX 1

Pool vegetation data, and pool types.

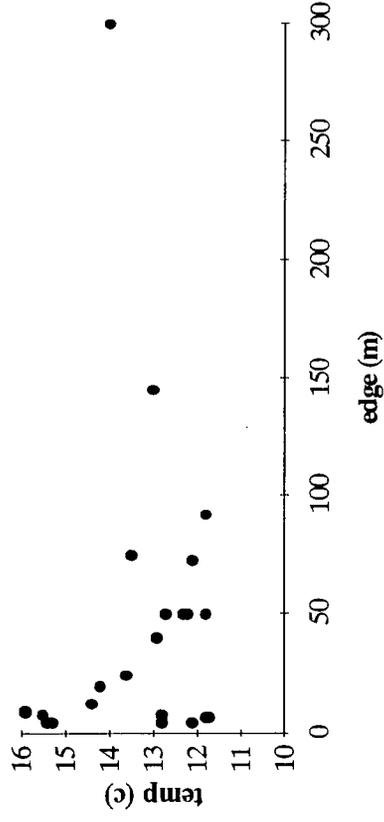
Site	Pool No.	Pool type	M. trifoliata	E. angustifolius	E. vaginatus	C. panicea	S. cuspidatus	S. palustre	S. papillosum	M. gallica	S. cespitosus	N. ossifragum	C. vulgare	P. purpureum	Algae	Leafy liverwort	D. intermedium	D. rotundifolium
LNC IA	1	B	0	3	0	3	2	3	0	0	2	0	0	1	0	0	0	0
	2	B	0	2	0	2	1	2	0	1	0	0	1	2	0	0	0	0
	3	B	0	0	0	3	0	2	0	2	0	0	1	2	0	0	0	0
	4	B	0	2	1	3	0	1	0	2	2	1	0	3	0	0	0	0
	5	D	4	2	0	0	2	2	0	2	0	0	0	1	2	1	1	1
	6	D	1	3	1	1	3	2	2	2	0	1	0	1	0	0	1	0
	7	B	0	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0
	8	A	0	3	1	0	5	2	0	0	2	1	0	0	0	0	0	0
	9	B	0	3	0	0	2	1	0	2	2	0	0	2	0	1	0	0
	10	B	0	2	0	0	0	0	0	1	1	0	0	1	0	0	0	0
	11	B	0	2	0	3	1	1	0	0	0	0	0	0	0	0	0	0
	12	B	0	2	0	4	2	2	0	0	0	0	0	0	0	0	0	0
	13	D	0	3	0	2	3	2	0	0	2	0	2	0	2	0	2	0
	14	D	3	2	2	0	2	2	1	0	0	1	0	2	2	1	2	1
	15	D	3	2	1	0	2	2	1	0	0	0	0	1	0	1	1	1
	16	D	3	3	0	2	2	2	2	2	0	1	0	2	1	2	2	1
	17	A/D	2	3	1	0	5	0	0	1	0	0	0	1	0	2	1	0
	18	B	0	2	0	0	2	2	0	2	2	0	0	1	0	1	0	0
	19	B	0	2	0	2	2	0	0	0	1	0	0	0	0	0	0	0
	20	B	0	2	0	3	2	0	0	0	0	0	0	0	0	0	0	0
	21	B	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	22	B	0	3	0	2	2	0	0	0	0	0	0	0	0	0	1	0
	23	B	0	3	0	2	2	0	0	3	2	0	0	1	0	0	0	0
LNC IB	24	A/B	0	4	2	0	4	2	0	1	0	0	0	0	0	0	0	0
2	25	A/B	0	4	0	0	5	2	0	1	0	1	1	0	0	0	1	0
3	26	A/B	0	4	1	0	5	2	0	0	0	1	0	0	0	0	0	0
4	27	A/B	1	3	1	0	5	1	0	1	0	0	0	0	0	0	0	0
5	28	A	1	3	3	0	4	3	0	1	0	1	0	0	0	0	1	0
6	29	D	3	1	0	0	2	2	0	0	2	1	0	2	0	2	0	0
7	30	A	0	3	2	0	5	1	0	1	0	0	0	0	0	0	1	0
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9	32	D	2	0	0	0	1	1	0	0	0	0	1	0	0	0	1	0
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14	37	D	3	3	0	0	2	1	0	0	0	2	0	2	2	0	1	0
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25	48	A/B	0	1	5	0	1	1	0	1	2	0	0	0	0	0	0	0
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27	50	B/A	0	2	3	0	4	1	0	1	1	1	0	2	0	0	1	0
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W IB	113	A/B	0	4	0	0	3	2	0	0	0	0	0	0	0	0	0	0
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10	122	D	2	1	0	0	2	2	2	0	0	0	0	3	2	2	1	0
11	123	A/D	1	2	0	0	4	2	0	0	1	0	1	3	1	1	1	0
12	124	D/A	3	2	0	0	3	1	0	0	0	2	0	0	0	1	0	0
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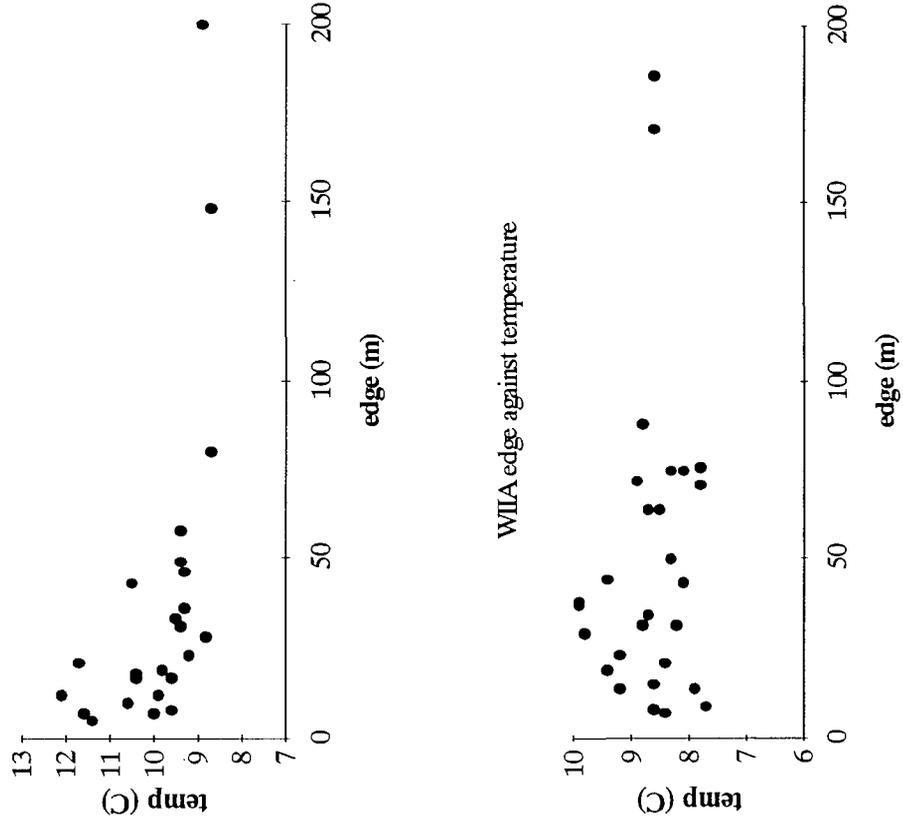
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4	137	A	2	3	0	0	5	1	0	2	0	0	0	2	0	0	0	
5	138	A	2	2	0	0	4	4	0	2	0	1	0	1	0	2	1	
6	139	A	2	3	0	0	5	2	0	2	0	0	0	1	0	0	0	
7	140	A	1	3	0	0	4	4	0	2	0	0	0	1	0	0	1	
8	141	A	2	2	0	0	4	3	0	2	0	0	0	2	0	1	1	
9	142	A	3	2	0	0	4	3	0	2	0	1	0	0	0	1	1	
10	143	A	3	2	0	0	5	2	0	1	0	0	0	1	2	2	1	
11	144	A	2	1	0	0	5	1	0	1	0	2	1	2	0	2	2	
12	145	A	3	2	0	0	5	2	0	1	0	1	0	2	0	2	1	
13	146	A	2	2	0	0	4	4	0	2	0	1	0	2	2	2	1	
14	147	A	3	1	0	0	5	2	0	1	0	1	0	2	0	1	1	
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16	149	A	3	2	0	0	5	2	0	1	0	2	0	1	0	2	1	
17	150	A	2	3	0	0	5	4	1	2	0	0	0	1	0	2	1	
18	151	A	3	2	0	0	5	3	0	1	0	1	0	1	0	2	1	
19	152	A	2	2	0	0	4	4	0	1	0	2	0	1	0	2	1	
20	153	A	3	3	0	0	4	4	0	0	0	2	0	2	0	2	1	
21	154	A	3	2	0	0	4	4	1	1	0	1	0	0	0	1	2	
22	155	A	3	3	0	0	4	1	0	1	0	1	0	0	0	3	1	
23	156	A	3	3	0	0	5	3	1	2	0	2	0	1	1	2	1	
24	157	A	3	2	0	0	5	2	1	2	0	2	0	1	0	2	1	
25	158	A	2	3	0	0	4	1	1	2	0	0	0	1	0	1	1	
26	159	A	2	3	0	0	4	4	1	2	0	0	0	0	0	1	1	
27	160	A	2	4	0	0	4	1	0	2	0	2	0	2	0	1	1	
28	161	A	2	4	0	0	3	3	0	2	0	2	0	1	0	1	1	
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2	163	A	1	3	0	0	4	2	0	2	0	1	0	1	0	1	0	
3	164	A	0	4	0	0	3	1	0	0	1	1	0	1	0	0	0	
4	165	A	2	3	0	0	4	1	0	0	0	1	0	2	0	1	0	
5	166	A	1	2	0	0	2	2	0	2	1	0	0	1	0	0	0	
6	167	A	2	3	0	0	4	3	1	2	0	1	0	1	0	1	0	
7	168	A	3	2	0	0	5	2	0	1	0	2	0	2	0	3	1	
8	169	A	2	1	0	0	4	4	0	1	0	2	0	1	0	2	1	
9	170	A	2	3	0	0	4	4	1	2	0	1	0	1	2	1	1	
10	171	A	3	2	0	0	5	4	0	1	0	1	0	1	3	1	1	
11	172	A	2	2	0	0	4	4	0	1	0	2	0	2	2	2	1	
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13	174	A	3	1	0	0	4	3	0	2	0	1	0	0	0	2	0	
14	175	A	2	3	0	0	4	3	1	2	1	2	0	1	1	2	1	
15	176	A	2	2	0	0	5	2	0	1	0	2	0	2	0	2	1	
16	177	A	3	1	0	0	4	1	0	1	0	0	0	1	1	2	1	
17	178	A	3	2	0	0	4	4	0	2	0	0	0	0	1	2	1	
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20	181	A	2	3	0	0	4	2	0	1	0	1	0	1	0	0	1	
21	182	A	3	2	0	0	3	4	0	2	0	1	0	1	0	1	1	
22	183	A	3	3	0	0	1	2	0	0	0	1	0	1	1	1	1	
23	184	A	2	2	0	0	1	4	0	1	0	1	0	1	2	1	1	
24	185	A	3	2	0	0	1	3	0	1	0	1	0	2	0	2	2	
25	186	A	3	3	0	0	2	4	0	2	0	2	0	1	0	2	1	
26	187	A	0	4	0	0	0	2	0	2	1	0	0	0	0	1	0	
27	188	A	0	4	0	0	0	1	0	2	2	0	1	0	0	1	0	

APPENDIX 2
Pool Variable plots

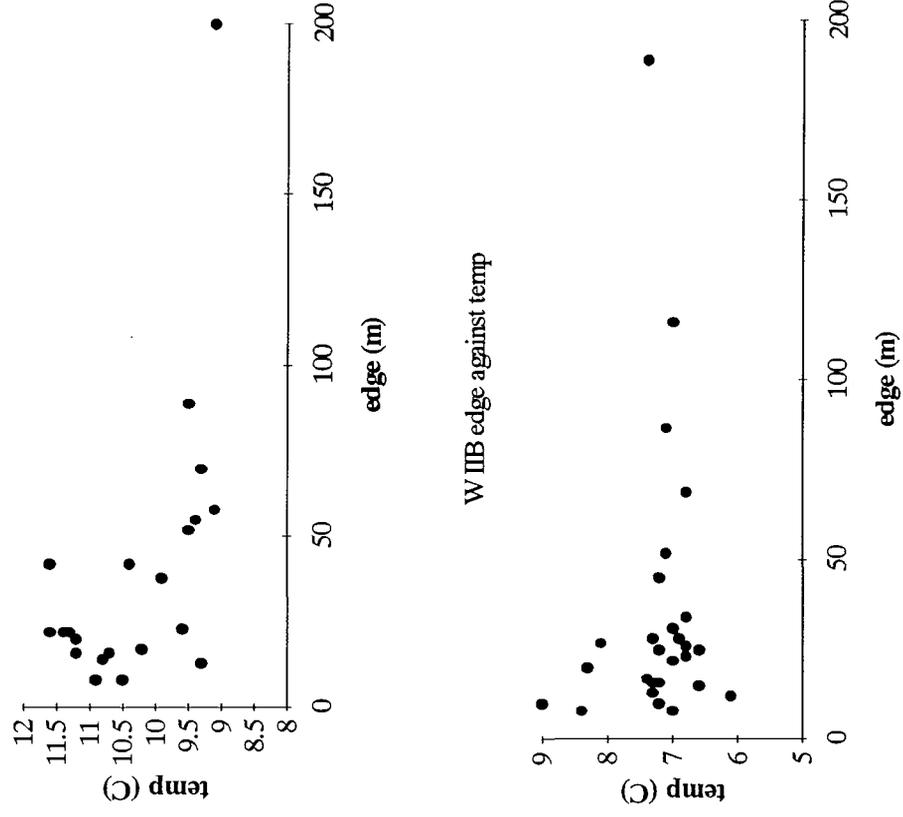
LNC IA edge against temperature



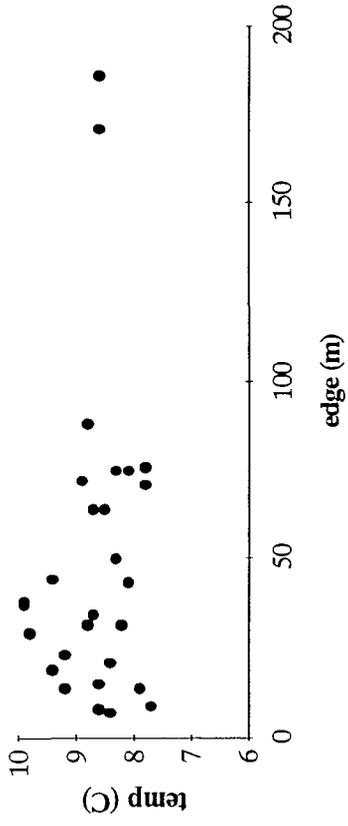
WIA edge against temperature



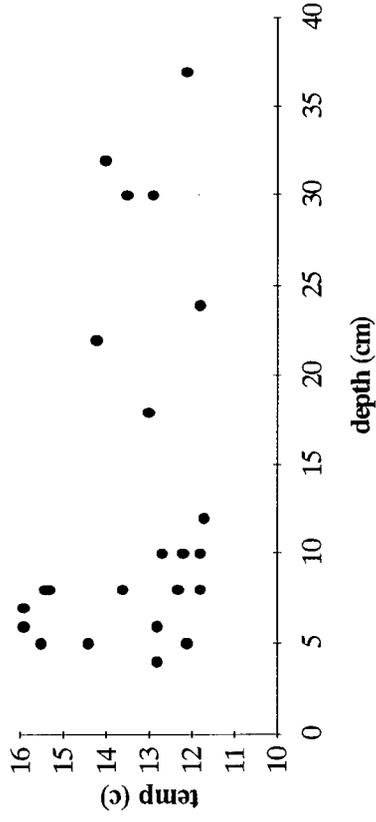
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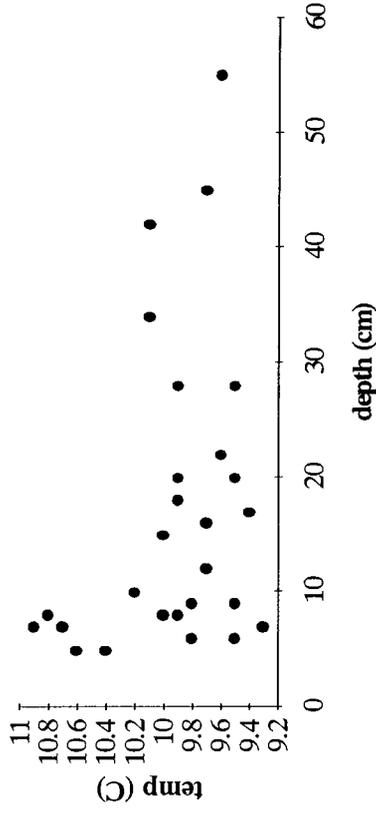
WIIA edge against temperature



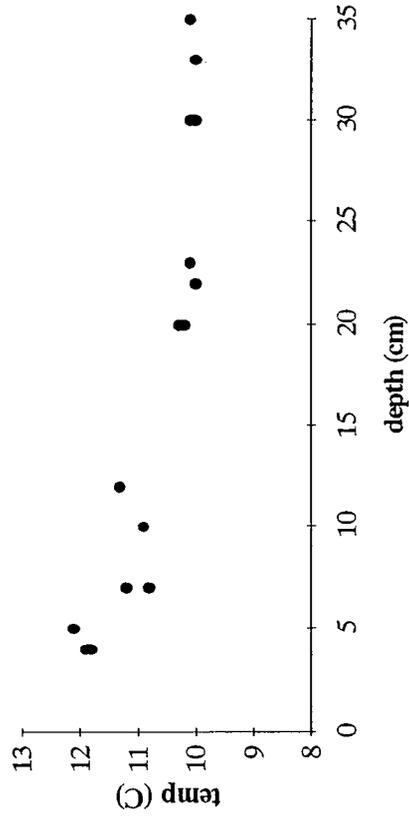
LNC IA depth vs temp



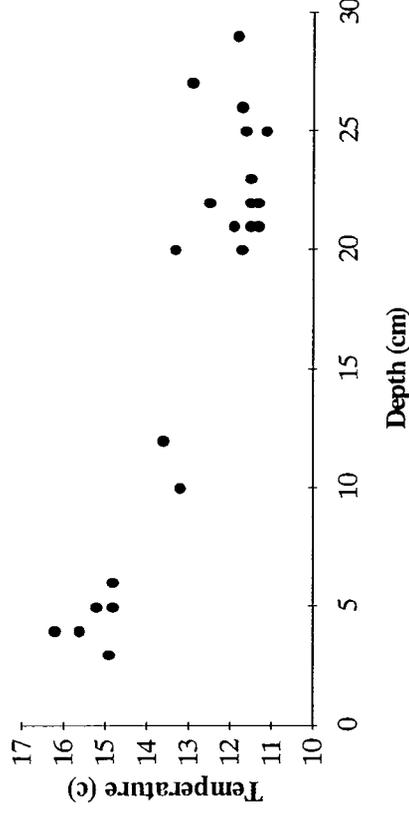
LNC IB depth against temp



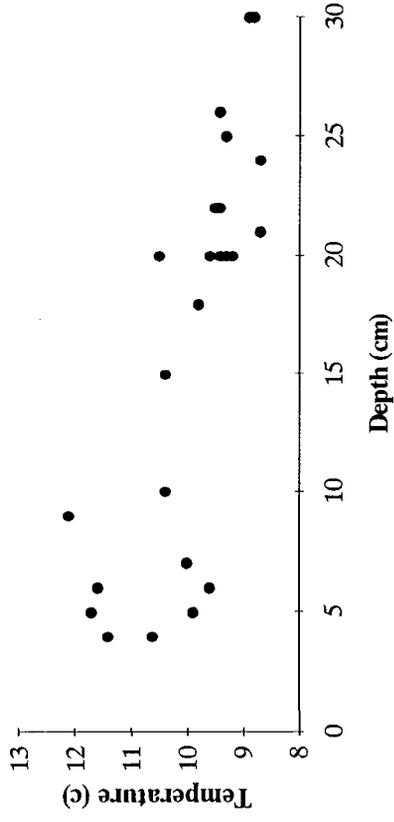
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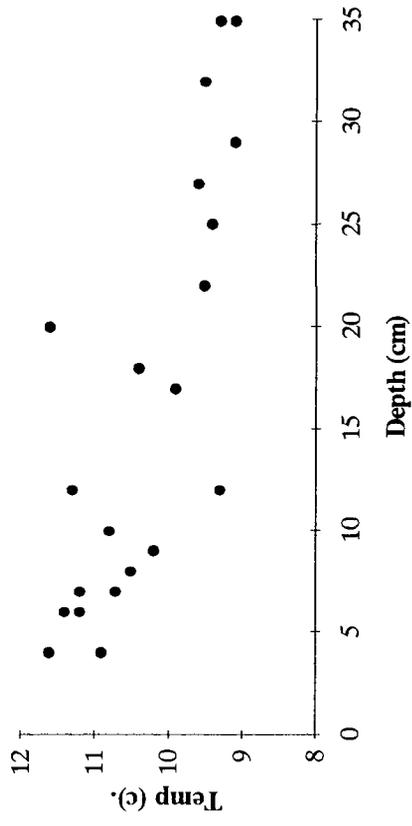
LNC IIB depth against temp (top,am)



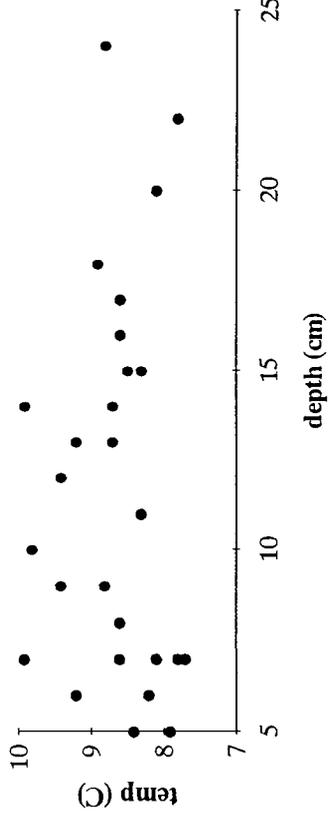
WIA depth/temperature (am,top)



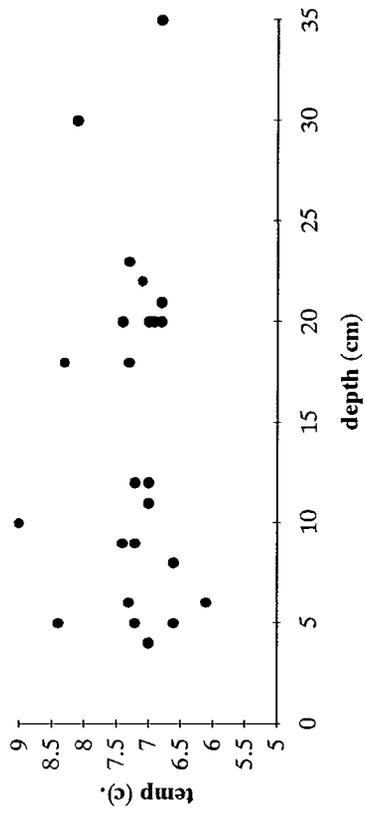
WIB depth against temperature



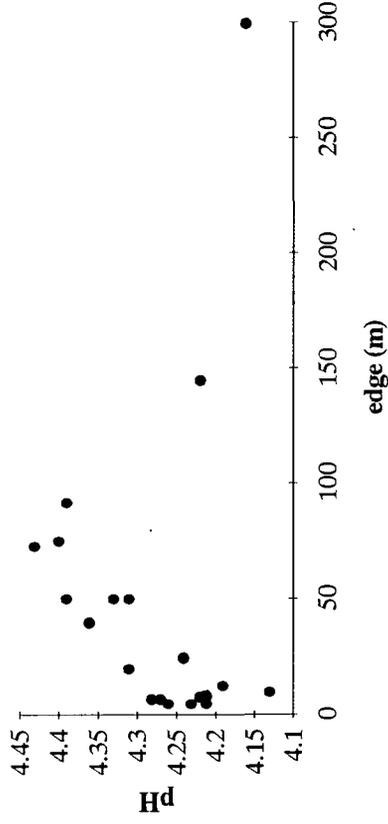
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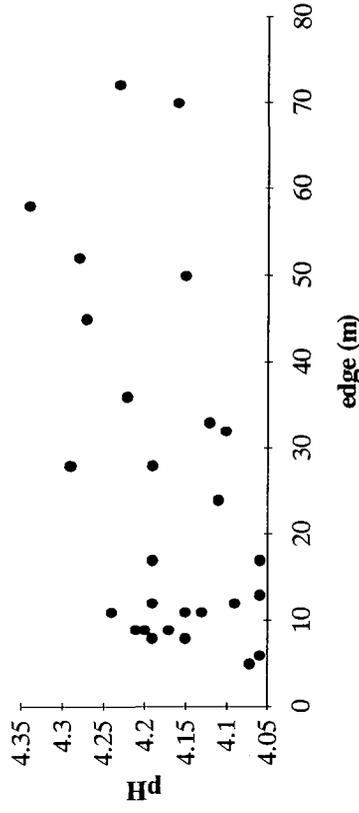
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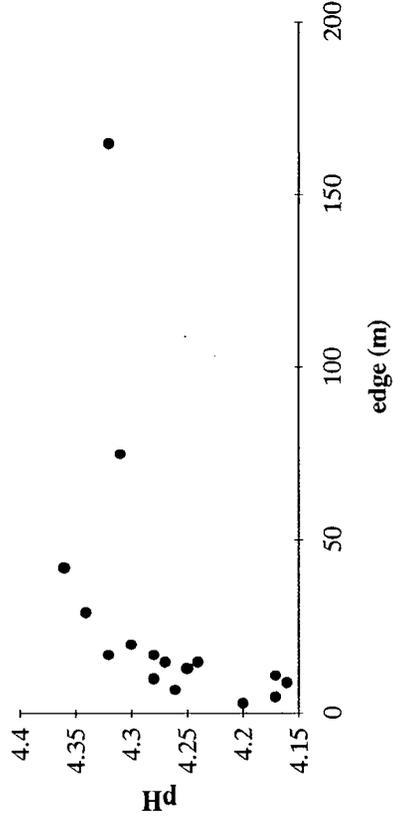
LNC IA edge against pH



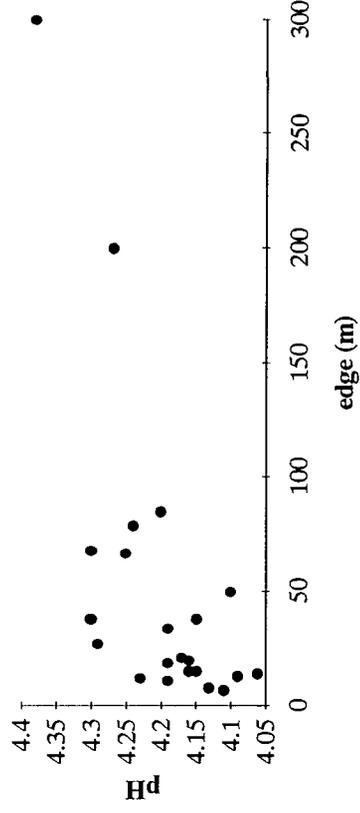
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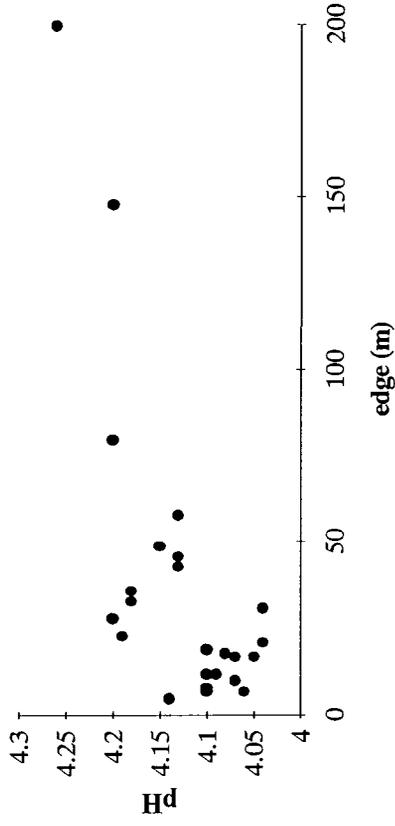
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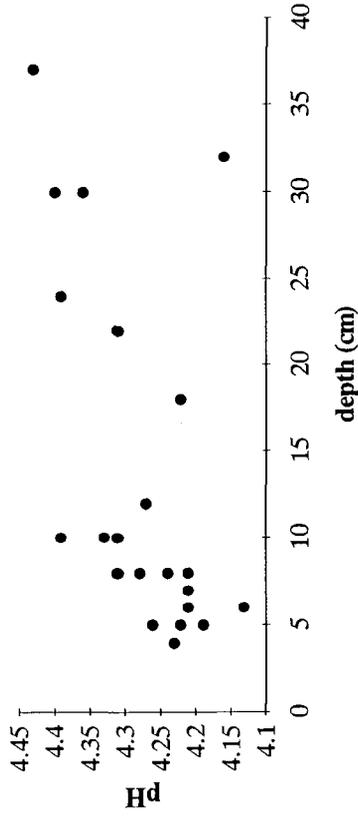
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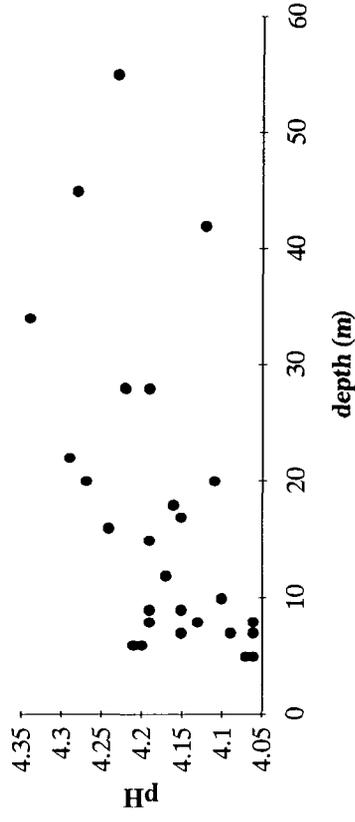
WIA edge against pH



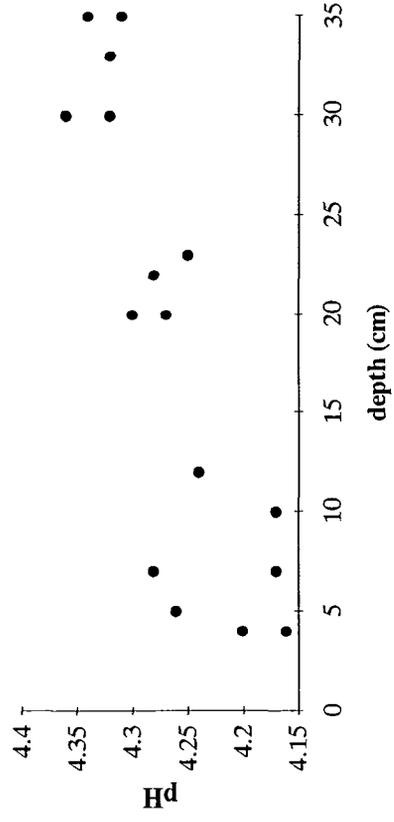
LNC IA depth against pH



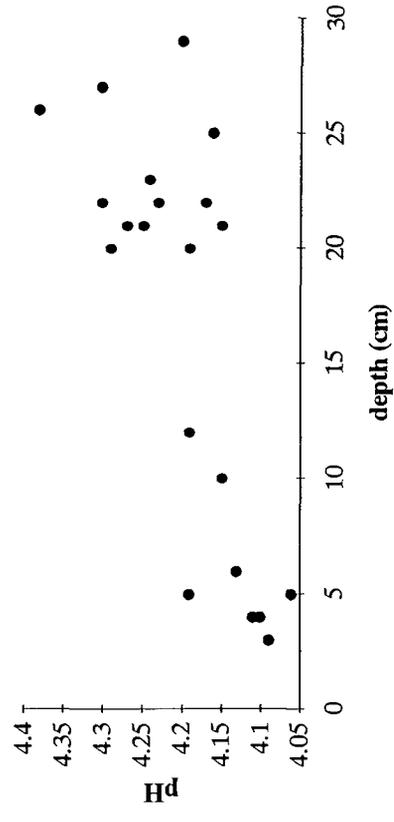
LNC IB depth against pH



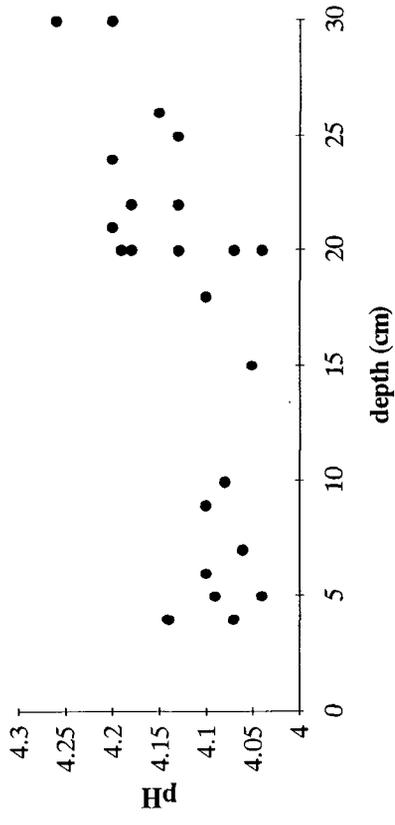
LNC IIA depth against pH



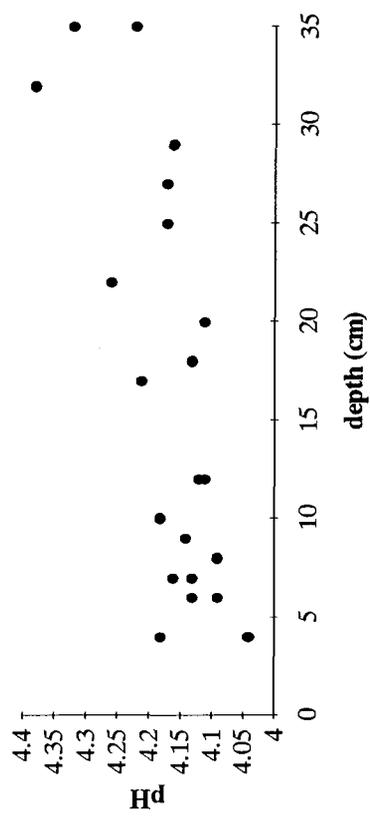
LNC IIB depth against pH



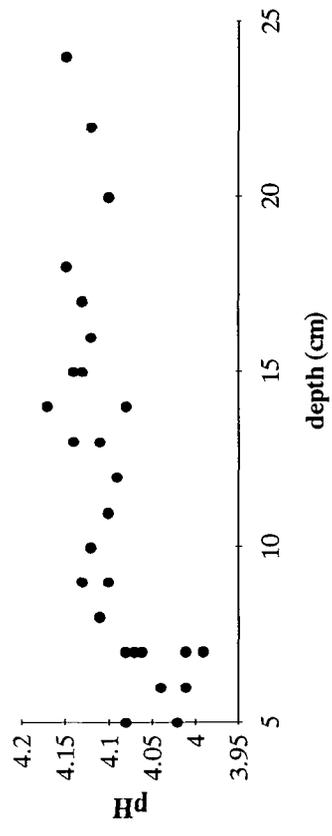
W IA depth against pH



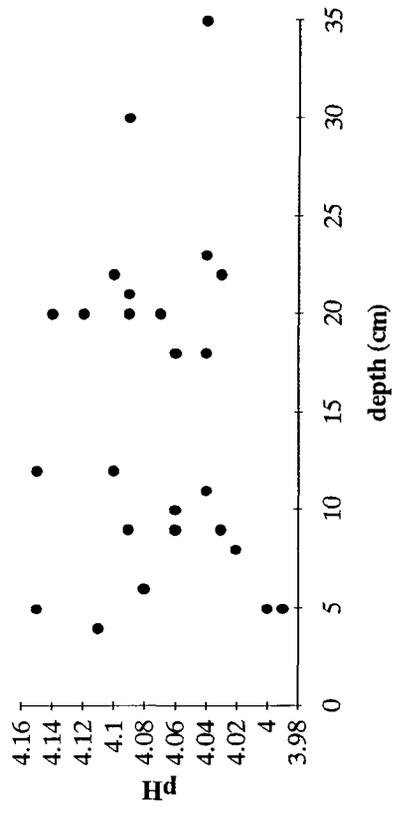
W IB depth against pH



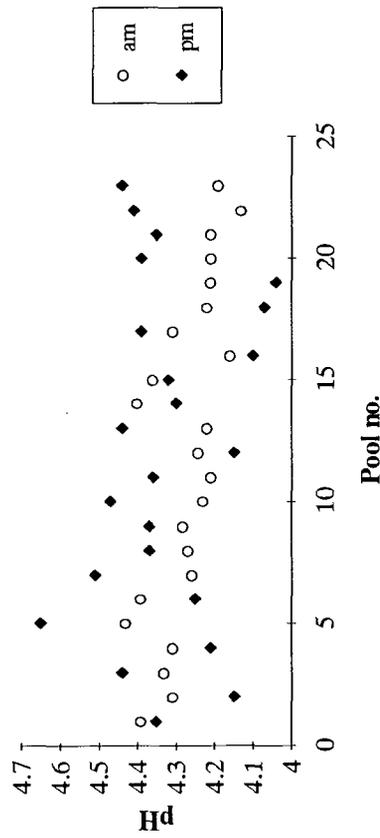
W IIA depth against pH



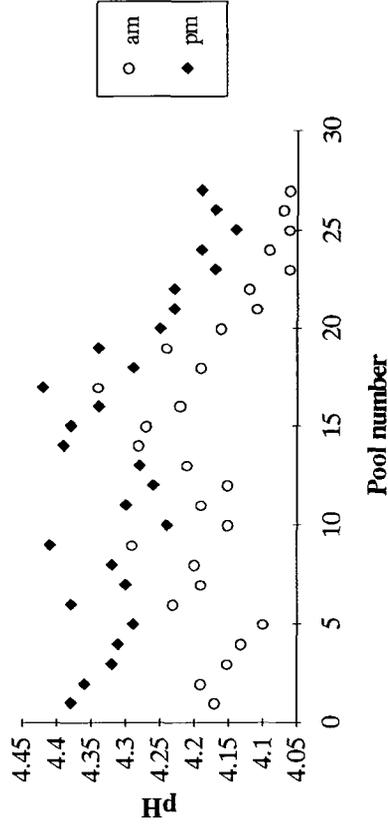
W IIB depth against pH



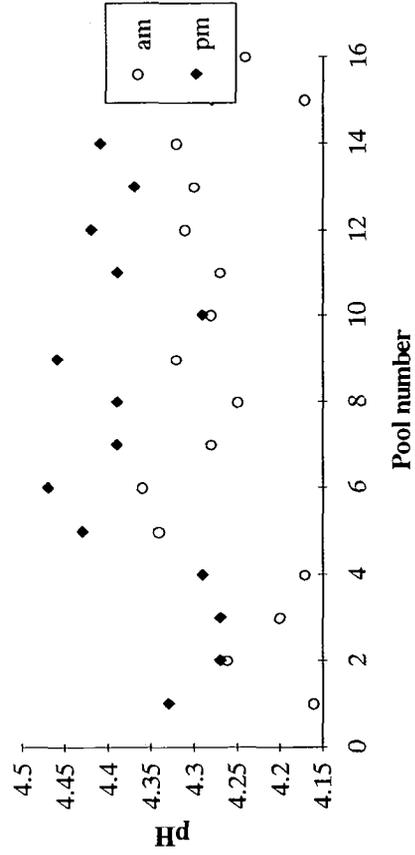
LNC IA pH am/pm (top)



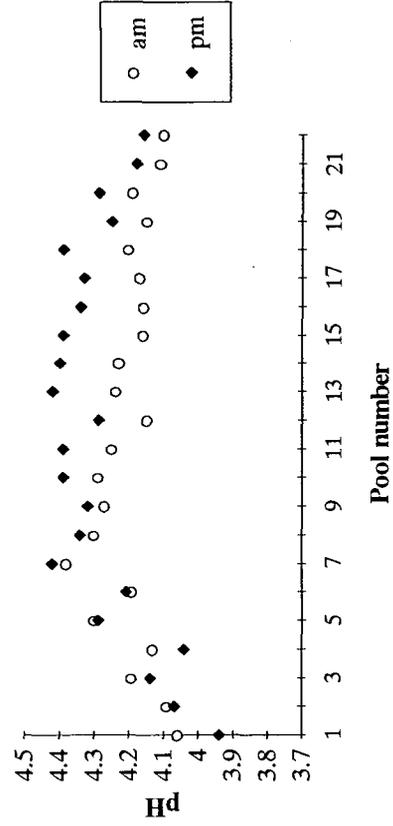
LNC IB pH am/pm (top)

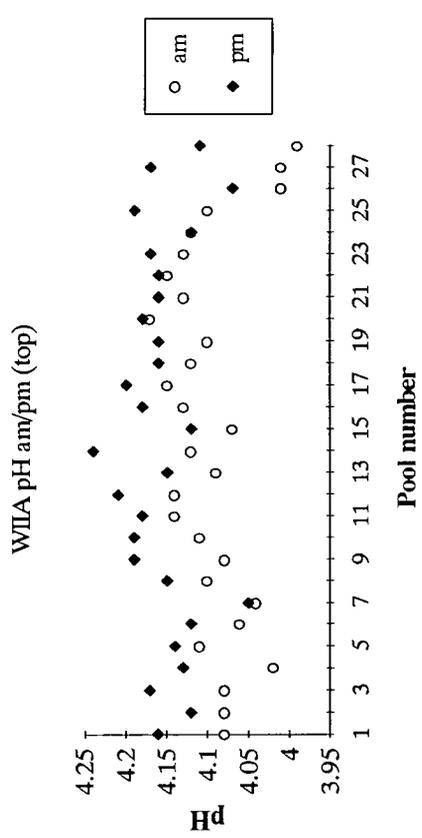
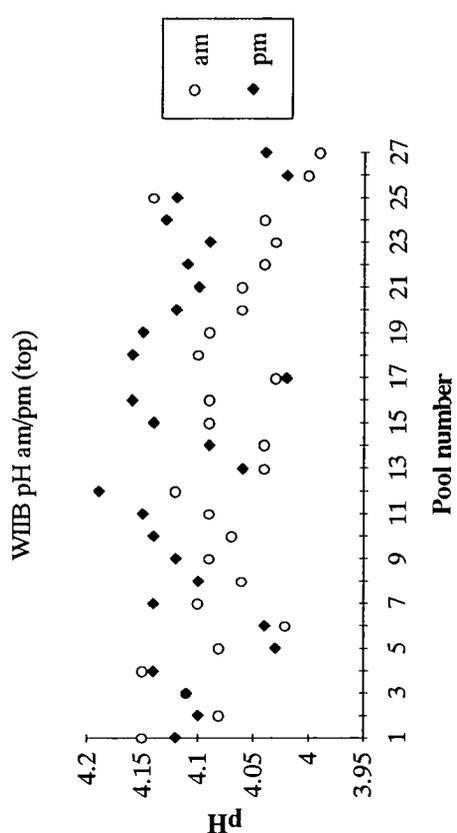
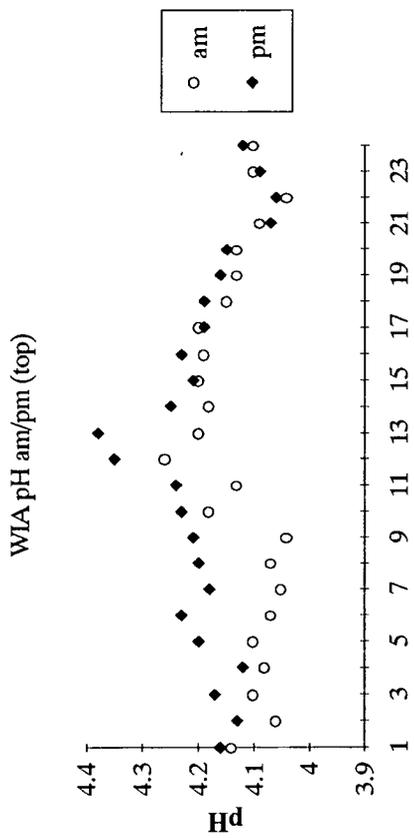
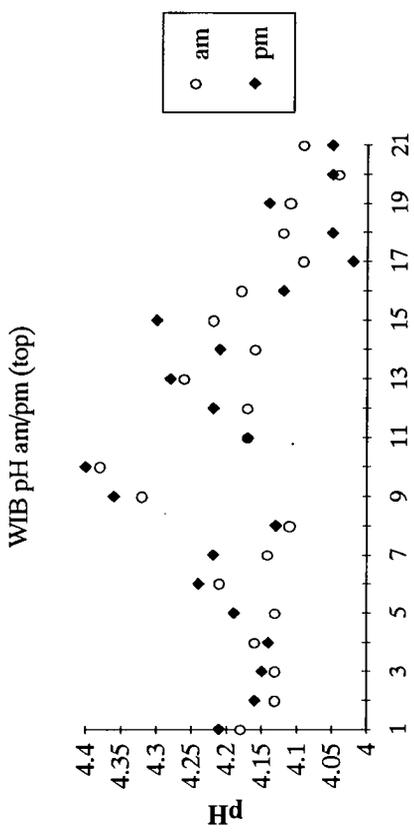


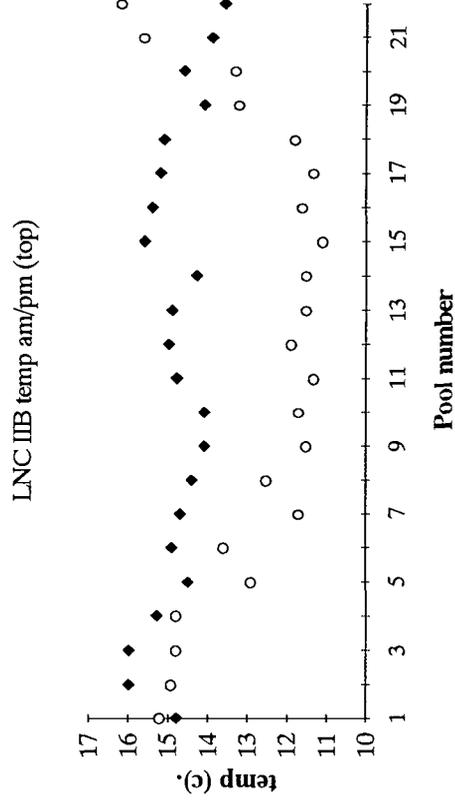
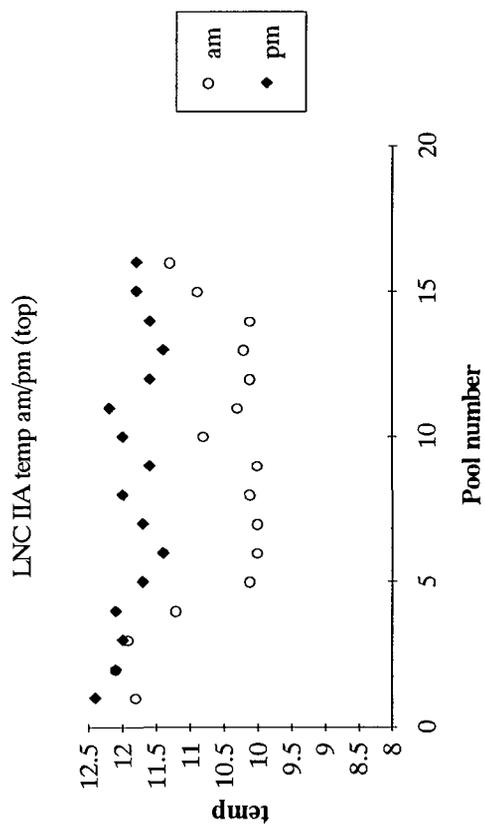
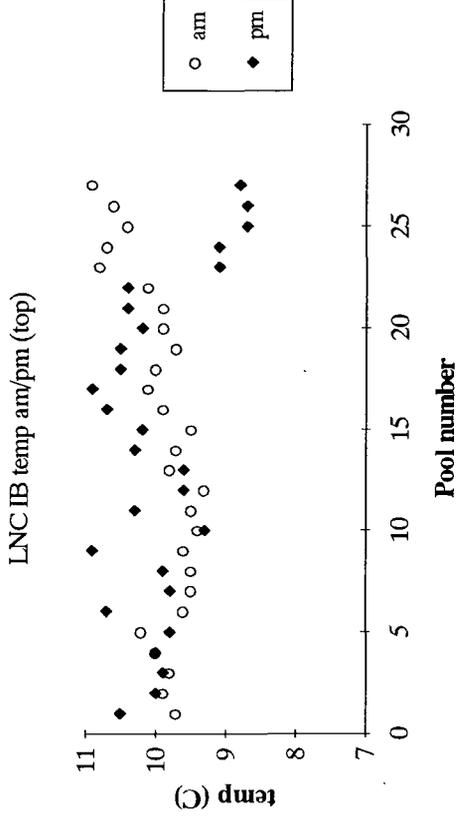
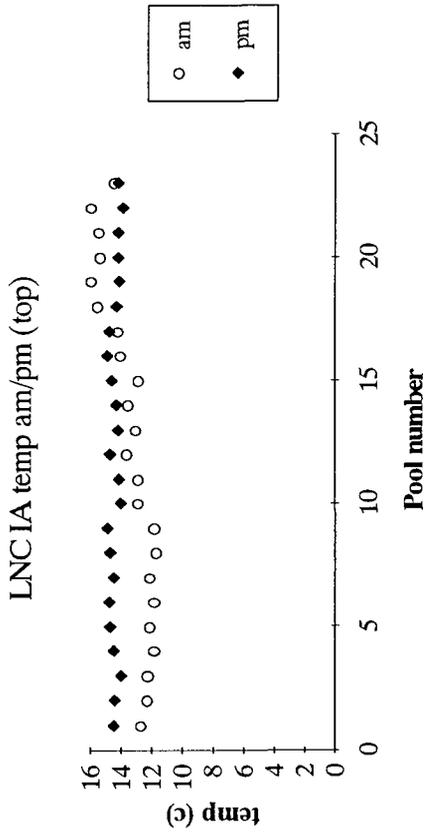
LNC IIA pH am/pm (top)

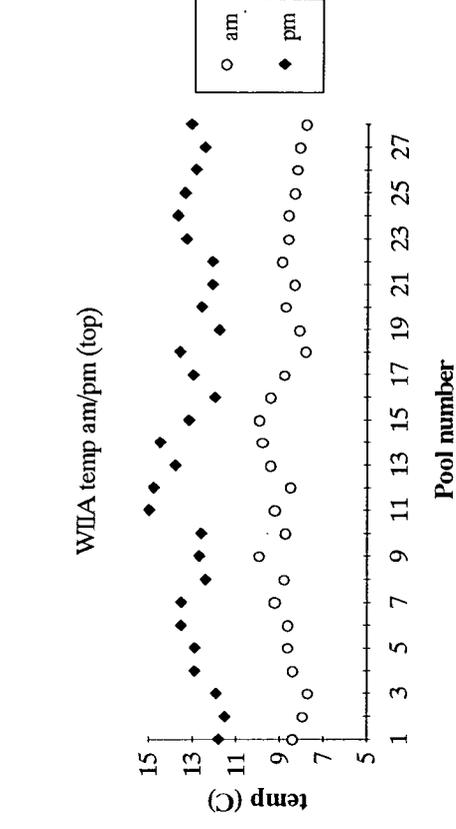
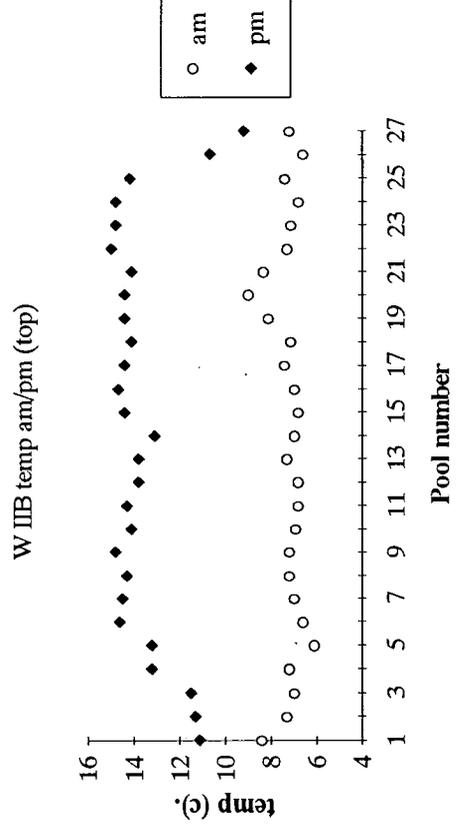
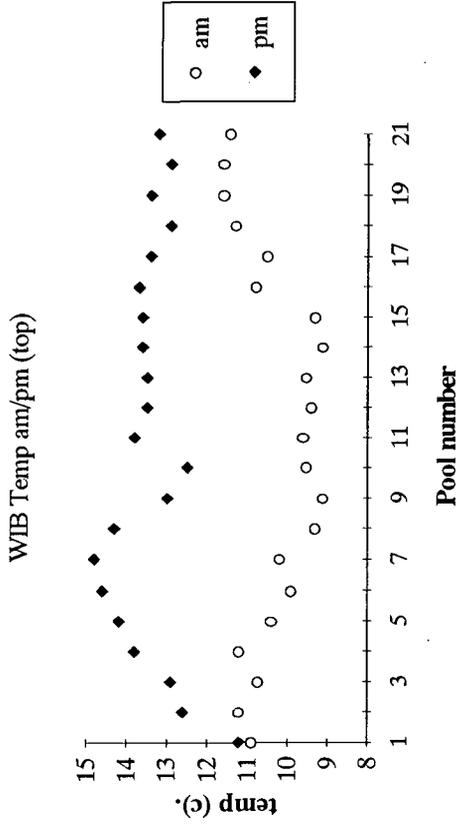
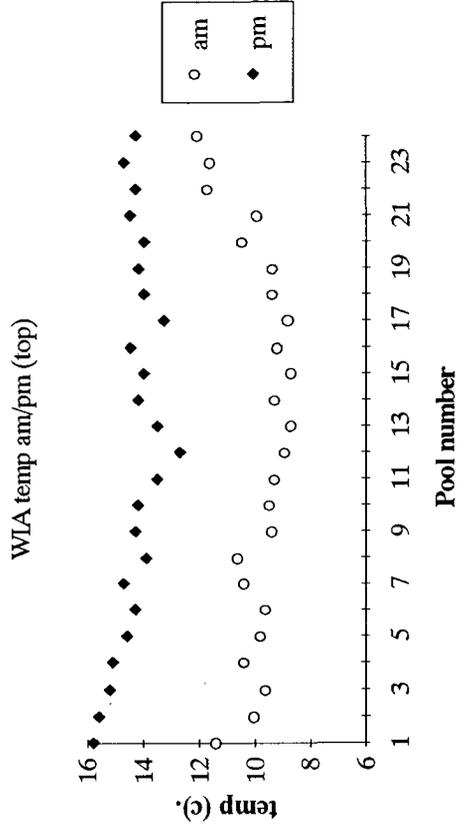


LNC IIB pH am/pm (top)









APPENDIX 3

Codes for families in DCA, CCA and TWINSpan analyses.

Species code number	Species code	Species/Family
1	FRO TAD	Frog tadpole
2	ADU NEW	Adult newt
3	JUV NEW	Newt larvae
4	NEW TAD	Newt tadpole
5	DYT SCD	<i>Dytiscidae</i>
6	CER ATO	<i>Ceratopogonidae</i>
7	CUL ICI	<i>Culicidae</i>
8	CHI RON	<i>Chironomidae</i>
9	CHA OBP	<i>Chaoboridae</i> (pupae)
10	CHA OBL	<i>Chaoboridae</i> (larvae)
11	DYT SCN	<i>Dytiscinae</i>
12	COR IXI	<i>Corixidae</i>
13	LIB ELL	<i>Libellulidae</i>
14	AES HNI	<i>Aeshnidae</i>
15	COE NAG	<i>Coenagriidae</i>
16	GYR INI	<i>Gyrinidae</i>
17	SIA LID	<i>Sialidae</i>
18	TRI CHO	<i>Trichoptera</i>
19	LEP TOP	<i>Leptophlebiidae</i>
20	PHR YGA	<i>Phryganeidae</i>
21	HYD RAC	<i>Hydrachnellae</i>
22	DIX IDA	<i>Dixidae</i>
23	LYC OSI	<i>Lycosidae</i>
24	FLY LAR	Fly larvae
25	TAB ANA	<i>Tabanidae</i>
26	NOT ONE	<i>Notonectidae</i>
27	HYD ROP	<i>Hydrophilidae</i>
28	LUM BRI	<i>Lumbricidae</i>
29	COL LAR	<i>Coleoptera</i> larvae
33	PLE COP	<i>Plecoptera</i>
31	COL LEM	<i>Collembola</i>
32	SPK CUL	Culicid type

APPENDIX 4

Mean depths and edges for pools with newts, and all pools, by site.

(i) Edges and depths of pools with newts, survey one. (Edges in metres, depths in cm).

Site	Pool No.	Newts	Depth (cm)	Edge (m)	Pool type
LNC I A	5	AdM Larv (2)	37	73	D
	13	AdF	18	145	D
	14	Larv	30	75	D
	15	AdF Larv	30	40	D
	16	Larv	32	300+	D
	LNC I B	6	AdF	55	72
9		Larv	22	28	D
11		Larv (4)	28	28	D
14		Larv (2) AdM	45	52	D
15		Larv (6)	20	45	AD
16		AdF	28	36	AD
17		AdM	34	58	D
LNC II A	5	Larv (4)	35	29	AD
	6	Larv (3)	30	42	D
	7	Larv (2)	22	17	A
	9	Larv	23	13	D
	12	Larv (2)	35	75	D
	13	Larv (5)	20	20	AD
	14	Larv	30	17	AD
LNC II B	5	AdM (2) Ad F (3) Larv (2)	27	68	D
	7	Larv (2)	26	300+	D
	9	AdM Larv (2)	21	200+	D
	12	Larv	21	38	D
	13	AdM	23	79	D
	14	Larv	22	12	AD
	15	Larv (4)	25	20	AD
	16	Larv (3)	25	15	AD
	17	Larv (2)	22	21	AD
	18	Larv (5)	29	85	AD
	20	Larv (3)	20	34	A
W I A	6	Larv (6)	20	17	A
	9	larv (2)	20	31	A
	10	AdF Larv (3)	22	33	A
	11	Larv (2) AdM	25	46	AD
	12	Larv (2)	30	200+	D
	17	Larv	30	28	D
	18	Larv	26	49	D
	19	Larv	22	58	A
	20	Larv (3)	20	43	A

W I B	5	Larv (3)	18	42	A
	9	Larv AdM	35	200+	D
	11	Larv	27	55	AD
	12	AdM Larv	25	23	AD
	13	Larv (2)	22	89	D
	15	Larv (2)	35	70	D
W I I A	17	Larv (3)	24	88	A
	19	Larv (2)	20	75	A
	24	AdM (2)	16	171	A
W I I B	10	Larv	20	28	A
	12	AdF	20	26	A
	14	Larv (2)	11	116	A
	15	Larv (2)	21	34	A
	16	Larv (6)	20	31	A
	18	Larv (3)	22	87	A
	22	Larv (2)	23	28	A
	24	Larv (3)	35	69	A
	25	Larv (3)	20	189	A

(ii) Edges and depths of pools with newts, survey two.

Site	Pool No.	Newts	Depth (cm)	Edge (m)	Pool type
LNC I A	5	AdM	37	73	D
	6	Tadp	24	92	D
	14	Larv (2)	30	75	D
LNC I B	6	AdM Larv (2)	55	72	D
	15	Larv (2)	20	45	AD
	17	Larv	34	58	D
LNC II A	5	Larv Tadp	35	29	AD
	6	Larv (3) Egg	30	42	D
	7	Larv Tadp	22	17	A
	9	Larv (2)	23	13	D
	12	Larv	35	75	D
	13	Tadp	20	20	AD
	14	Larv (2)	30	85	AD
LNC II B	5	Tadp	27	68	D
	7	Larv (2)	26	300+	D
	8	Larv	22	38	D
	9	Larv	21	200+	D
	13	Larv	23	79	D
	14	Larv	22	12	AD
	15	Larv	25	20	AD
	18	AdF AdM Tadp	29	85	AD
	20	Larv (3) Tadp	20	34	A
		Larv			

W I A	6	Larv (8)	20	17	A
	9	Larv (2)	20	31	A
	10	Larv (2)	22	33	A
	11	AdM (2)	25	46	AD
		Tadp			
		Larv			
	12	Larv (4)	30	200+	D
	18	Larv	26	49	D
19	Larv (2)	22	58	A	
20	Larv (2)	20	43	A	
W I B	5	Larv	18	42	A
	9	Larv (3)	35	200+	D
	12	Larv	25	55	AD
	13	Larv	22	89	D
		AdM			
W I I A	12	Tadp	15	64	A
	18	Tadp	22	76	A
	20	Tadp	14	64	A
W I I B	10	Larv (3)	20	28	A
	12	AdF	20	26	A
	14	Larv (3)	11	116	A
	15	Larv	21	34	A
	16	Larv	20	31	A
	18	Larv (2)	22	87	A

(iii) Mean edges and depths of pools with newts and all pools, surveys one and two.

Site	Mean depth all pools with newts, survey one	Mean depth all pools with newts, survey two	Mean depth all pools	Mean edge all pools with newts, survey one	Mean edge all pools with newts, survey two	Mean edge all pools
LNC I A	29.4	30.33	13.61	126.6	80.0	45.74
B	33.14	36.33	17.30	45.57	58.33	25.41
LNC I	31.58	33.33	15.6	79.33	69.17	34.76
LNC II A	27.86	27.86	18.56	30.43	30.43	28.31
B	23.73	23.89	16.95	79.23	92.89	51.86
LNC II	25.34	25.63	17.63	60.25	65.56	41.95
W I A	23.89	23.13	16.0	56.11	59.63	38.76
B	27.0	25.0	16.43	79.83	96.5	40.33
W I	25.13	23.75	16.2	65.60	71.92	39.44
W I I A	20.0	17.0	11.5	111.33	68.0	50.32
B	21.33	19.0	14.44	67.56	53.67	36.00
W I I	21.0	18.33	12.95	78.50	58.44	43.29

APPENDIX 5

Availability and utilisation of pool types by newts.

Site	Pool type	Total number	Number with newts	% used
LNC I	B	22	0	0
	A	11	0	0
	AD	4	2	50
	D	13	10	76.9
LNC II	B	12	0	0
	A	6	2	33.3
	AD	9	8	88.9
	D	11	8	72.7
W I	B	6	0	0
	A	24	6	25
	AD	5	3	60
	D	10	6	60
W II	B	0	-	-
	A	55	12	21.8
	AD	0	-	-
	D	0	-	-
Total	B	40	0	0
	A	96	20	20.8
	AD	18	13	72.2
	D	34	24	70.6

APPENDIX 6

Time spent sampling in each pool type and newt captures.

Site	Pool type	Effort (minutes)	Newts caught, survey	
			one	two
LNC I	B	158	0	0
	D	248	18	7
	A	73	0	0
	AD	63	7	2
LNC II	B	67	0	0
	D	211	20	11
	A	52	5	2
	AD	92	25	10
W I	B	35	0	0
	D	172	9	9
	A	122	18	15
	AD	241	8	7
W II	B	-	-	-
	D	-	-	-
	A	743	30	11
	AD	-	-	-

APPENDIX 7

Newt sizes

(i) Adults, survey one.

Total length (mm)	Snout - Cloaca (mm)	Tail : Body ratio
Males		
64	34	0.88
69	39	0.77
69	38	0.82
71	38	0.87
67	36	0.86
70	37	0.89
68	36	0.89
67	37	0.81
64	36	0.78
63	34	0.85
64	35	0.83
69	37	0.86
62	34	0.82
Females		
73	36	1.03
79	48	0.98
72	38	0.89
73	44	0.66
73	43	0.70
72	37	0.95
68	36	0.89
75	40	0.88
71	37	0.92

(ii) Adults, survey two.

Total length (mm)	Snout - Cloaca (mm)	Tail : Body ratio
Males		
66	35	0.89
62	34	0.82
68	37	0.84
59	36	0.64
73	40	0.83
68	38	0.80
Females		
76	40	0.9
77	42	0.83

(iii) Larvae, survey one.

Total length (mm)	Snout - cloaca (mm)	Total length (mm)	Snout - cloaca (mm)
33	11	35	17
35	17	39	18
37	18	37	18
34	15	28	13
33	16	42	21
34	15	37	18
38	18	39	19
35	16	37	17
35	17	32	16
26	14	33	15
31	16	38	18
25	12	43	21
30	15	39	19
41	20	39	18
42	20	33	16
33	15	37	18
31	16	44	20
21	13	32	15
34	17	36	17
31	17	36	16
32	15	23	12
37	17	40	18
41	20	35	16
32	16	35	18
24	11	35	16
42	22	35	16
34	16	37	17
46	23	29	14
36	19	34	11
36	17	27	18
38	18	28	15
36	17	36	19
39	19	33	10
39	18	28	13
33	16	35	17
37	18	34	16
28	14	40	19
42	20	36	19
40	20	42	19
32	15	37	17
34	16	40	21
34	16	19	10
37	18	35	17
37	17	28	14
31	15	36	18
32	16	26	13
35	16	32	16
32	17	35	17

37	18	35	17
27	13	28	14
37	18	38	18
35	17	31	15
24	12	28	14
34	17	32	16
32	15	29	14
30	15	37	18
30	16	27	14
34	16	22	11
24	12	21	14

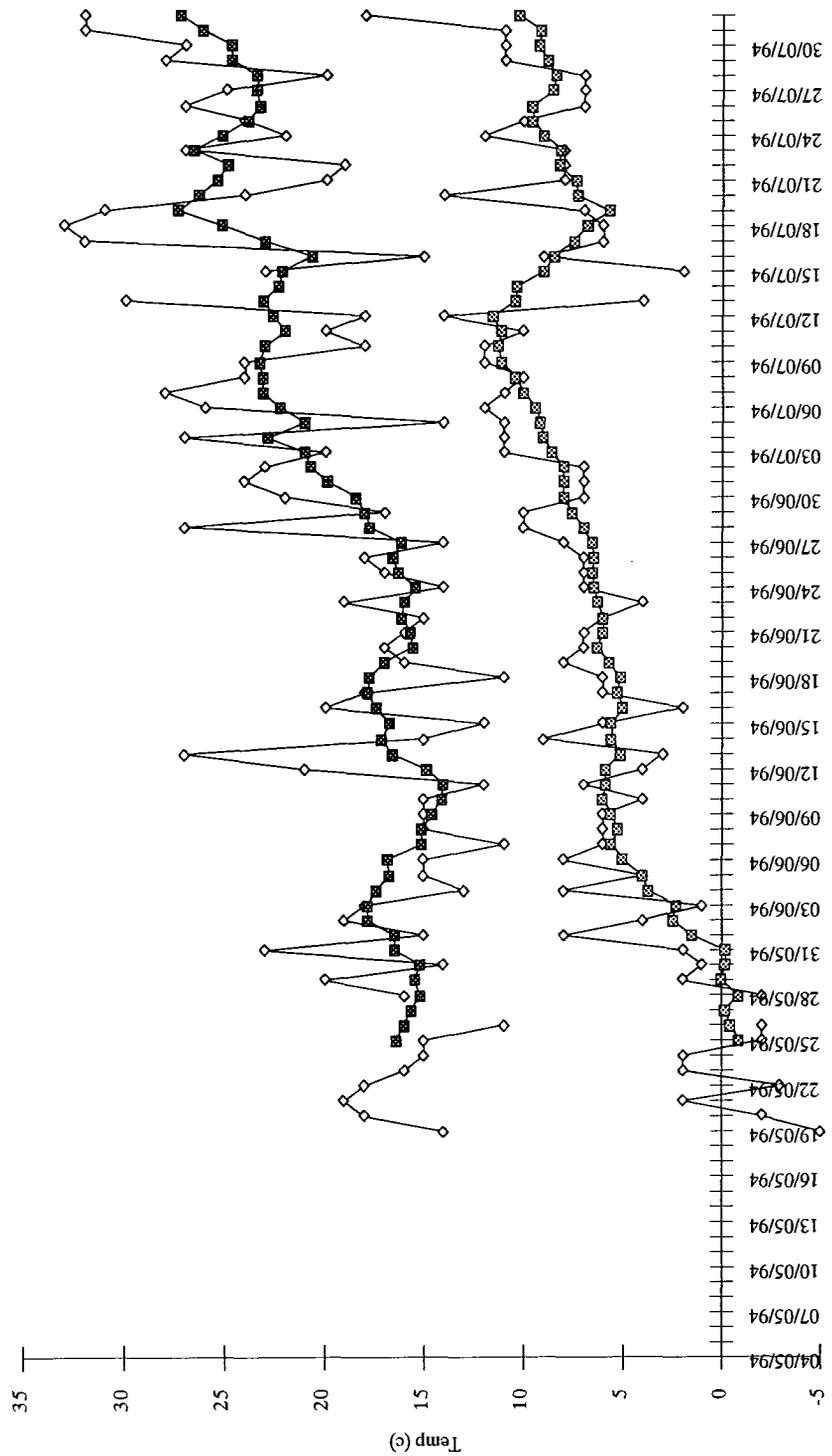
(iv) Larvae, survey two.

Total length (mm)	Snout - cloaca (mm)	Total length (mm)	Snout - cloaca (mm)
34	18	42	21
30	15	43	21
32	16	35	17
33	17	41	18
32	17	36	17
35	18	38	18
35	18	38	18
32	16	39	20
34	18	39	21
38	19	36	17
35	17	37	17
36	18	40	19
31	15	38	16
37	19	38	18
44	22	31	17
43	22	39	18
42	21	37	18
38	19	36	18
35	18	36	17
35	17	32	16
30	17	40	20
37	18	37	18
32	16	35	17
39	20	35	18
38	19	29	14
36	18	30	15
31	15	37	18
38	19	31	16
35	17	34	18
36	19	38	19
37	19	36	18
32	17	37	18
37	20	39	20

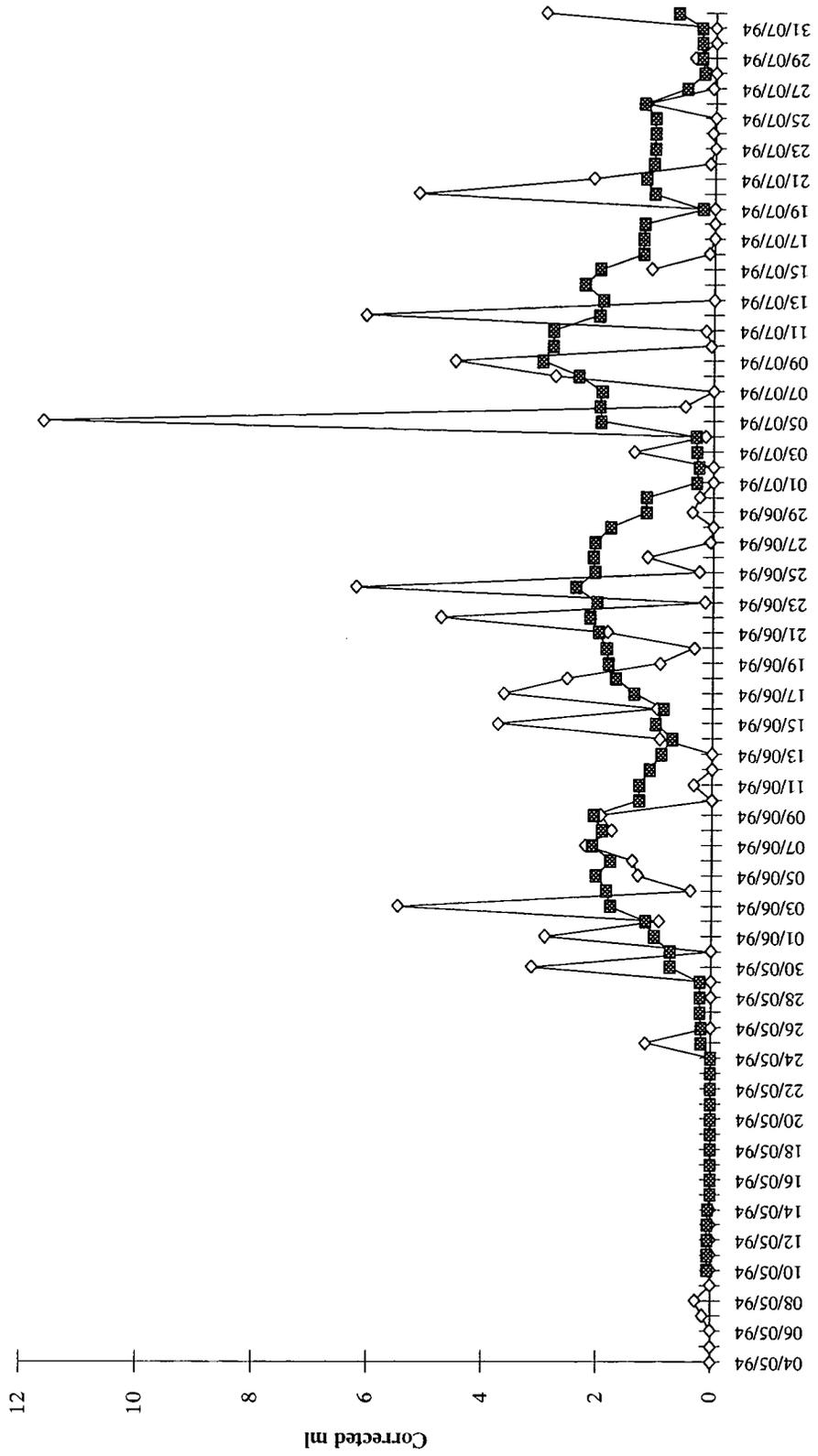
(v) Pitfall data; Juveniles. Snout-cloaca lengths in brackets.

Date	Size (mm)	Date	Size (mm)
30/6/94	43 (23)	11/8/94	42 (22)
	41 (22)		20 (21)
	36 (20)		38 (20)
Also; 62 (33) sub-adult caught			35 (21)
13/7/94	No juveniles caught		37 (19)
29/7/94	37 (21)		40 (21)
	38 (20)		41 (20)
	37 (18)		38 (19)
	39 (21)		41 (21)
	37 (19)		40 (20)
	40 (21)		34 (18)
	36 (19)		40 (22)
	44 (22)		43 (24)
	41 (22)		39 (20)
	39 (20)		40 (21)
			43 (24)

APPENDIX 8: Meteorological data: (i) Minimum and Maximum temperatures (moving average)



(ii) Rainfall (adjusted with moving average)



APPENDIX 9

Pool invertebrate data, and pool types.

Site	Pool No.	Pool type	Dytis cidae	Cera topogoni dae	Culic idae (pupae)	Chironomida e (larvae)	Chob (pupae)	Chob (larvae)	Dytis cidae	Corixidae	Libellulidae	Aeshnidae	Coenagrionidae	Gyrinidae	Sialisidae	Trichoptera	Leptophlebiidae	Phryganeidae	Hydrachnellae	Dixidae (pupae)	Lycosidae	fly larvae	Notoptera dae	Tabanidae	Hydrophilidae	Lumbrici dae	Coleoptera larvae	Plecoptera	Collembola	Culicid type
LNC IA	1B		18	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2B		9	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	3B		3	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	4B		8	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0
	5D		0	0	0	2	1	36	1	13	1	3	5	3	5	1	12	3	0	0	0	0	0	0	0	0	0	0	0	0
	6D		3	0	1	2	0	12	0	5	1	3	0	0	0	1	19	0	0	0	0	0	0	0	0	0	0	0	0	0
	7B		6	0	3	7	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	8A		5	1	2	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	9B		6	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	10B		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	11B		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	12B		6	0	0	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	13D		1	0	2	2	0	5	0	4	0	1	0	0	0	0	25	0	0	0	0	0	0	0	0	0	0	0	0	0
	14D		0	0	1	1	0	8	0	14	0	0	1	2	0	1	19	21	0	0	0	0	0	0	0	0	0	0	0	0
	15D		0	0	0	4	0	5	0	11	1	1	6	0	0	2	37	1	0	0	0	0	0	0	0	0	0	0	0	0
	16D		0	0	3	3	0	4	0	18	1	1	3	0	1	0	12	4	0	0	0	0	0	0	0	0	0	0	0	0
	17A/D		5	0	1	22	0	22	0	9	0	2	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0
	18B		4	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
	19B		2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	20B		3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	21B		2	0	0	6	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
	22B		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	23B		16	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
LNC IB	24 A/B		3	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	25 A/B		3	0	0	1	0	0	3	0	0	0	0	0	0	2	5	0	0	0	1	0	0	0	0	0	0	0	0	0
	26 A/B		3	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	27 A/B		0	1	0	3	0	0	2	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	28 A		2	0	0	7	0	0	3	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	29 D		3	0	2	3	0	42	0	10	0	2	2	0	0	4	3	0	0	0	0	0	0	0	0	0	0	0	0	0
	30 A		1	0	0	2	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0

