ASPECTS OF THE ECOLOGY OF

TWO SPECIES OF CENOCORIXA (CORIXIDAE: HEMIPTERA)

IN ALLOPATRY AND SYMPATRY

by

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ABSTRACT

Facets of the biology of the sibling species <u>Cenocorixa</u> <u>bifida</u> and <u>C</u>. <u>expleta</u> (Corixidae) were compared in different habitats, constituting both sympatric and allopatric populations. The study aimed to identify reasons for the differing distribution of the two species. In particular, it sought to (a) explain why and how the species coexisted over part of their range in lakes of moderate salinity, and (b) deduce why <u>C</u>. <u>expleta</u> is absent from the more freshwater lakes.

The thesis is divided into six sections. An introduction, reviewing competition theory and summarising the problem, is followed by studies on the environments investigated, in Chapter II. Chapter III discusses distribution, abundance and breeding pattern of the corixid species encountered, to obtain data relevant to certain indirect measures of competition, and Chapters IV and V describe feeding experiments and serological gut analyses of field-collected corixids. The feeding experiments aimed to obtain one measure of the fundamental niche, while the gut enalyses were carried out for a measure of the realised niche. The final section discusses the findings in terms of potential species interaction.

The study area comprised six lakes on Becher's Prairie, in the Chilcotin area of B.C., and another near Kamlccps; all lakes were similar in general morphology. Although temperature patterns were similar between lakes, they varied considerably in conductivity. Temperatures and conductivity data corroborate

earlier findings, suggesting that the studied years were not atypical.

Oxygen levels and phytoplankton primary production were generally higher in the more freshwater lakes, but the contribution of aquatic macrophytes and benthic algae there was not measured. Phytoplankon production was restrained. Plankters were abundant in all lakes, especially inshore, but the levels fluctuated most in the three freshwater lakes, being very low there before mid-June. Diaptomid copepods and fairy shrimps were confined to the higher salinity lakes, while chaoborids and amphipods were restricted to the three freshwater lakes; other invertebrates were widely distributed. Both biomass and diversity of organisms were highest in the freshwater lakes, but they were by no means low in the saline lakes studied. The data suggest that there was an abundance of food in all lakes at all times.

C. bifida bred in all lakes investigated, although excluded apparently through increasing salinity from Lake LB 2 after spring. C. expleta bred sympatrically with C. bifida in waters of over 6000 umhos cm^{-1} conductivity, whereas Cymatia americana, Hesperocorixa laevigata, Callicorixa audeni and Sigara sp. bred only in the three most freshwater lakes. C. expleta produced three generations a year in the highest salinities (LB 2 and Barnes Lakes) and two in other high salinities. C. bifida produced two generations a year in the higher salinities, but like all the other corixids, in the three most freshwater lakes often produced only one generation a year. Corixids showed no

definite trends of different abundance with alkalinity, and the two species of _Cenocorixa_ did not show depressed population levels in sympatry. Further, the phenology was essentially contemporary in sympatry.

C. expleta when allopatric occurred in both marginal and mid-lake areas, whereas _C. bifida_ when allopatric was more confined to the littoral areas. In both species, habitat preferences of instars varied with season, but in general the largest individuals of each species preferred the most complex environments. Overall, _C. expleta_ in sympatry was relatively commonest over deeper waters and over plain mud or silt, whereas _C. bifida_ preferred rocks, logs and reeds. However, the segregation was not marked.

Both _C. bifida_ and _C. expleta_ took a wide variety of preys offered in experiments. _C. expleta_ adults accepted more of the preys offered than did _C. bifida_ . Juveniles showed less marked species differences than did adults, and accepted prey more often than them. Both species accepted both live and dead organisms. Juveniles of both species preferred dead prey to live; however, only for _C. expleta_ was this trend significant overall.

When offered live or dead mixed plankton, _C. bifida_ took chiefly ceriodaphniids, whereas _C. expleta_ took both diaptomids and ceriodaphniids in the proportions offered. In other choice situations, both species fed more often on chironomids than daphniids, taking zygopterans least. However, unsuccessful attacks were far more frequent on daphniids than on the benthic

and littoral organisms. In summary, the experimental feeding results suggest that the fundamental niches of the two species of Cenocorixa are similar, but not identical.

Guts of field-collected corixids were analysed by serological techniques using 10 active antisera. Most reactions indicated a clearly carnivorous habit, less than 1% being positive for algae. Results suggest that foods eaten varied dynamically between instars, lakes and seasons. In C. bifida daphniids and zygopterans were more frequently recorded in guts from the sympatric lakes than from the freshwater lakes. Ephemeropterans and amphipods were identified chiefly from summer-collected corixids, and were chiefly restricted to the freshwater lakes, paralleling their distribution. However, some reactions were also seen in guts from these lakes with diaptomid antiserum, perhaps a reaction to other copepod species.

In C. expleta most positive results were seen for daphniids in spring and fall corixid samples. More male than female C. expleta took ephemeropterans, and more male than female C. bifida took zygopterans. Specific differences between saline and freshwater lakes seemed to relate to prey distribution, but in Lake LB 2 C. expleta took significantly more diaptomids in fall than in summer. In sympatry, most juveniles of both species took an increeasingly diverse diet with increasing instar size, although the preferred order chironomids, then zygopterans, ephemeropterans and diaptomids, remained relatively constant. Second instar C. expleta reached a plateau level of feeding intensity only reached by third instar C. bifida ; this seems

related to instar size. In larger instars, C. bifida showed more serological reactions with most foodstuffs than C. expleta .

Overall, C. expleta showed more positive reactions than C. bifida with chironomids and daphniids, but less with diaptomids and zygopterans. In sympatry, C. bifida fed more on daphniids and ephemeropterans than in allopatry, which tends to contradict ideas of competition for food. The serological data suggest that the realised niche with respect to feeding is not markedly more restricted than the fundamental niche.

Other corixid species had similarly carnivorous diets, C. audeni showing more reactions for amphipods and chironomids than H. laevigata , but less for chaoborids, suggesting more benthic orientation for the former.

In field-collected corixids, red guts usually contained diaptomids, while brown guts reacted with a variety of antisera. In several brown and olive guts there was no serological reaction, indicating that the antisera did not cover the total dietary range. Occasional guts were bright blue-green, suggesting cyanophyte material.

Despite a wide geographical overlap between the species, C. bifida and C. expleta possess somewhat different osmotic and ionic regulatory capacities, and show slightly different habitat and food preferences. Therefore they cannot be considered as true ecological homologues, and hence competition need not necessarily result in exclusion of one or other. With regard to habitat, some of the differences observed may be related to

variation in the environments between lakes studied, but other differences show the species not to be identical. C. expleta seems to have a rather wider fundamental niche in terms of habitat than C. bifida , but neither show marked restriction in sympatry.

The serological feeding results suggest that in sympatry, each species took different proportions of the same foodstuffs. The realised niches appear somewhat restricted from the fundamental niche data obtained from feeding experiments. C. expleta seemed somewhat more specialised in feeding than C. bifida , thus fulfilling the requirements of an included niche species; again a point usually considered to permit coexistence. However, diet and habitat preferences of species and instars varied with season and lake, suggesting that pooling data obscures much of the real variation.

In general, the evidence shows that the two species of Cenocorixa are not exact ecological homologues, and competition between them in sympatry was not evident. The reason for the absence of C. expleta from the more freshwater lakes, to which it appears physiologically suited, still remains obscure.

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CHAPTER I. INTRODUCTION

Natural systems are dynamic in nature. Fauna and flora are
continually changing in abundance and distribution. The
distribution and abundance of a species may thus alter from year
to year as well as with seasonal environmental changes, and the
results of field sampling usually represent only a moment in a
dynamic process.

Many studies of species interactions assume that they are
concerned with end-point situations (vide DeBach, 1966); the
result of invasion of a new habitat, or the outcome, in the form
of elimination of one species, of competition between related
forms. However, it is equally likely that an intermediate stage
in either process would be encountered over the time span of
most studies.

Competition between species is fundamental to many
ecosystems, even at equilibrium (here defined as showing minor
oscillations which do not affect ecosystem structure or
function). Where a necessity of life, commonly food or shelter,
is limiting, superior life forms will eventually crowd out those
less well adapted, whether conspecifics or members of a related
species. Results in the field are most obvious in the latter
case, end-point situations being represented by absence of one
faunal element from an area where it apparently could survive.

During studies by Scudder (1969b) of the fauna of a series
of saline lakes of differing alkalinity in central British
Columbia, two species of the water bug genus _Cenocorixa_ were

observed to coexist in certain water bodies but not in others. Their breeding ranges appeared to follow the salinity gradient, C. expleta (Uhler) being restricted to waters of higher salinity, and C. bifida hungerfordi Lansbury to the more freshwater lakes, where it coexisted with other breeding corixid species.

Because of their pronounced dispersal at certain times of year both species occasionally occur in lakes outside their breeding range, but sympatry in breeding populations was only seen in lakes of from 6000 to 12000 μmhos cm⁻¹ average conductivity (Scudder, 1966). The distribution and osmotic and ionic balance in the two species of Cenocorixa were examined by Scudder (1969a) and Scudder et al. (1972), and all evidence to date indicates that both are osmotically freshwater species. However, although C. expleta is physiologically capable of living in the lower salinity lakes, it does not occur in them naturally. Thus, Scudder et al. (1972) suggest that this absence of C. expleta from various freshwater lakes is not likely due to an inability to survive in those waters.

It is suggested that ecological factors, such as predation, availability of suitable food, and interspecific competition among others, may be important in explaining the absence of C. expleta from the lower salinity lakes. However, to date this has not been demonstrated, although Jansson (1971, 1972b) has suggested a possible difference in habitat preference of the species.

This thesis is thus concerned with an appraisal of some of

the ecological factors that have been suggested as perhaps important in the apparent exclusion of C. expleta from the lower salinity lakes. In particular, availability of suitable food, feeding preference and feeding interaction in these two species of Cenocorixa are considered, with data obtained both in the field and the laboratory. In addition, the relative abundance of the two species in allopatry and sympatry and their phenology was studied for an assessment of competitive interaction. The fundamental and realised niches in the two species are both assessed and discussed.

THE CONCEPTS OF COMPETITION, COMPETITIVE INTERACTION AND COMPETITIVE EXCLUSION

Competition has been adequately reviewed several times, perhaps best by Crombie (1947), Hardin (1960), DeBach (1966), Miller (1967) and Darlington (1972). The concept of competitive exclusion has been inherent in biological thinking since Darwin hinted at it as a corollary to the struggle of existence (1864). Grinnell (1904) among other early authors (vide Udvardy, 1959) stated that "...two species of approximately the same food habits are not likely to remain long enough evenly balanced in numbers in the same region; one will crowd out the other...". In the 1920's the ideas were formally demonstrated by the use of set theory and calculus (Lotka, 1925; Volterra, 1926). Gause (1934, 1935), after whom the principle of competitive exclusion has sometimes been named, produced the first experimental

evidence in support of it, using simultaneous equations to verify his findings mathematically.

Since then there have been many attempts to test the principle. For example, MacArthur and Levins (1967) verified the mathematics of Volterra (1926), but it would appear that the principle is not amenable to disproof, since while evidence can be adduced to support it (i.e. Crombie, 1947), seemingly contradictory results only invite a more careful study of the conditions of sympatry and overlapping niches in the field or laboratory. Thus, in one sense, the principle remains a trivial, self-evident axiom (Ayala, 1970). However, it relates closely to the ideas of the struggle for existence in another sense; competition is likely to be most intense between conspecifics, resulting in the survival of the fittest individual, whereas in less closely related groups one whole species, race or other taxon may succumb competitively to another in a particular habitat, and the results will be demonstrable above the level of the individual. This has been discussed by DeBach (1966), amongst others.

The concept of competition itself has been revised repeatedly. Miller (1967) reviews the progress made in these redefinitions and refinements, and points out the two major components of competition; exploitation, which is the effective utilisation of a resource, alone or shared; and interference, where resource utilisation is less efficient under competitive situations than by species alone, in allopatry. Interference may be direct (behavioural territoriality in passerines is an

obvious example), or indirect, where one species degrades the environment or food source through its activities, making it less acceptable to the other.

The generally accepted definition of competition was stated by Crombie (1947) as "...the demand, typically at the same time, of more than one organism for the same resources of the environment, in excess of immediate supply...", and other authors (i.e. Larkin, 1956; Weatherley, 1963) in general, accept that species interaction, if it is to be labelled as competition, must share a common resource. An opposite school, starting with Nicholson (1933), feel that only the criterion that survival decreases as density increases, is needed to justify use of the term 'competition'. This 'extended competition' includes parasitism and predation, and any interaction between organisms, no matter how complex or indirect, that is, or may be disadvantageous to any of them, must be included (Darlington, 1972).

Problems in the definition of the 'niche' are summarised by Elton and Miller (1952) and by Weatherley (1963). Following Elton (1927), who used the term in the sense of a 'profession' such as 'scavenger', Weatherley (1963) and many others described the niche as based on the nutritional role of the animal in the ecosystem, reasoning that food is the most likely facet of the environment to be in short supply. On the other hand, Grinnell (1917) and others saw the niche as essentially an 'address'; a division of the habitat which is a smaller component of, but not fundamentally different from, an ecosystem. This raises the

question of the term 'sympatric', which is usually used in a geographic, large-scale sense but which could logically be used to connote coexistence in any environmental division from the micro-ecological scale up to the geographic.

The 'address' concept of the niche is unsuited to competition studies, since it is highly probable that many species will coexist in the smallest measurable environmental division. Thus we require a conceptual model which will "...accomodate both the functional and distributional concepts..." (Miller, 1967). Hutchinson came close to this in describing the niche in terms of set theory as an 'n-dimensional hyperspace' (Green, 1971), and Milstead (1972), in an attempt to quantify the niche for comparative purposes assessed the contributions and importance of reproductive strategy, physiological and biological responses to adverse conditions, foods and feeding, predation, adaptation and so forth. Together these comprise the total natural history of each organism.

A further complication is the distinction between 'fundamental' niches - those defined by observations of the species in allopatry and in laboratory surveys - and 'realised' niches; those observed in nature in each instance. Where the realised niche is smaller or more restricted than the fundamental, some form of interference or exploitation competition must be invoked as an explanation. This provided the starting point in the present study, since the fundamental niche for the Cenocorixa species in terms of salinity tolerance was larger than that observed in the British Columbia lakes studied.

To confirm interspecific competition, one must show significant overlap in fundamental niches, including showing that in sympatry the realised niche is smaller than in allopatry (Miller, 1967).

Paralleling the historical development outlined above, there has been much redefinition of the principle of competitive exclusion, or, as DeBach (1966) would prefer, the "principle of competitive displacement". Hutchinson (1965) restated the principle as "...closely allied species living together practically always occupy slightly different niches, or, in other words, have different tolerances and optima". This is certainly a masterpiece of evasion. Even a frequently accepted summary of the principle, "complete competitors cannot coexist", is likewise totally ambiguous (Hardin, 1960) and further lacks a clause dealing with inequalities in reproduction. Clearly each term needs precision.

Ayala (1969, 1970) investigated two _Drosophila_ species which reached a steady state coexistence although one species was more successful in the larval stage, and the other as adults. He considered that his results experimentally invalidated the principle, but the resource 'niche' involved was not adequately defined and Gilpin and Justice (1972) decided that his findings were in harmony with the theoretical work in Gause and Witt (1935). Gause (1970) also felt that Ayala's experiment replicated one of his own 1935 experiments, where two apparently competing _Paramecium_ species were in fact exploiting largely different niches, one chiefly in the liquid medium of a

culture feeding on bacteria and the other predominantly eating yeasts at the bottom. Gause himself restated the principle in 1970 to read "two species competing for limited resources can only coexist if they inhibit the growth of the competing species less than their own". All authors admit the term 'niche' needs clarification.

A further problem with coexistence is the possibility that interspecific association may be a function of other factors (assessed by Cole, 1949, 1954) such as mutual attraction; one species seeking out the other as prey or for other reasons; or both being attracted or repelled either by another species or by an environmental situation.

Darlington (1972) has restated Gause's principle in a form that is valid without exception, as "...two populations or species cannot long coexist if they compete for a vital resource, limitation of which is the direct and only factor limiting both populations". Where resource competition does not lead to extinction of one party, populations are limited by separate density-dependent factors, so that the resource is not fully utilised. Darlington points out that although many plants compete for light, they coexist, and there is surprisingly little adaptive radiation to utilise different wavelengths. Thus, although even light falling at the earth's surface is theoretically a limited resource, other factors are actually limiting and so are competed for first.

Similarly, Stanley's (1973) cropping principle, which states that predation allows greater diversification of prey

species, is thus not an invalidation of the principle of competitive exclusion, since predation by reducing numbers of a formerly victorious species can lead to under-utilisation of a resource, and hence competitors can coexist. Stated as above by Darlington, the principle of competitive exclusion needs no further testing. However, the time element is now explicitly mentioned, and the real interest in and significance of the principle now becomes more obvious, in that it indicates that under certain conditions, coexistence can occur in many habitats. Recorded examples of such coexistence are surveyed by Miller (1967) and the factors permitting them are analysed.

MacArthur and Levins (1964) looked at a hypothetical patchy environment and pointed out that related species avoided competitive elimination through size or habitat differences; pure specialist (coarse-grained) species, such as predators taking large prey, do not usually interact or affect each other and so may coexist; whereas species specialising in a particular proportion of two or more resources will be eliminated if that proportion should change significantly. Most mixed-resource species are found in stable communities. Hairston (1959) also observed that in a multi-species community the less successful species are only found in very suitable, restricted areas, thus their distribution appears clumped. On the other hand, successful species are more numerous and less clumped, and appear closer to a random distribution. This is related to Miller's (1967) ideas of 'included niches' where two competitors have overlapping niches, one inside the other's.

MacArthur (1958) and Slobodkin (1962) conclude that most of today's communities are near equilibrium; the ecological principles discussed above apply to these but not necessarily to altered or early successional stages. However, this statement might need qualification. In a recent study, Grenney et al. (1973) used a theoretical model of a phytoplankton population to explain the observed coexistence of many algal species in an apparently homogeneous environment, in terms of a continual variation in environmental conditions with time. Thus, the population never really attained competitive equilibrium, although tending towards different equilibria at different times. Similarly, Stewart and Levin (1973) showed mathematically that in a seasonally changing environment, conditions for stable coexistence may be met when two or more species compete for one or more resources, thus contradicting certain forms of the competitive exclusion principle. It seems that ecological conditions of competition in 'stable' and 'fluctuating' environments may need separate theoretical analysis.

THE CORIXIDAE : THE ANIMALS TO BE STUDIED

Corixids as a group have been the subject of a large body of research, in part related to their occurrence in a wide range of habitats, their abundance, and their dispersal patterns. Several authors, such as Hungerford (1919), Macan (1938, 1962) and Istock (1973) consider them to be particularly suited to studies of species interactions, chiefly for these reasons of

distribution and abundance.

Much work has been done on corixid distribution patterns in different habitats, often in relation to the water chemistry, habitat facies and other species present (i.e. Brocks and Kelton, 1967; Brown, 1948; Knowles and Williams, 1973; Lansbury, 1960; Macan, 1938, 1949, 1954a, 1954b, 1962; Martin, 1970; Pajunen, 1970a; Popham, 1952; Sailer, 1948; Savage, 1971; Scudder et al., 1972). Oloffs and Scudder (1966) discussed an aspect of this; the irreversible effect of high temperature, such as may be found in shallow or temporary ponds, upon cuticular wax and waterproofing.

The permanence and suitability of the habitat has been related to dispersal and migration tendencies in many studies, notably those of Brown (1951) and Pajunen (1970b), and many authors have discussed its relationship with the incidence of alary polymorphism and consequent flightlessness (i.e. Leston, 1953; Johnson, 1960, 1963, 1966; Macan, 1939; Pajunen and Jansson, 1969b; Popham, 1943, 1952, 1959, 1964; Popham and Lansbury, 1960; Richard, 1958, 1966; Southwood, 1961; Southwood and Johnson, 1957; Scudder, 1964, 1971; Scudder and Meredith, 1972; and Simpson, 1968). Johnson (1963, 1966) considered the effect of physiological factors such as the quality and length of the pre-oviposition period on the regulation of migratory flight.

Other studies have dealt with corixid life history phenomena, such as population structure and annual production (i.e. Ancona, 1933; Crisp, 1962a; Istock, 1973; Popham, 1952;

Jansson and Scudder, 1974) while the last-named authors and Crisp (1962b), Johnson (1963), Martin (1970, 1972), Pajunen (1970a, 1970c), Savage (1971) and many others discussed aspects of corixid development, oviposition and ovarian arrest, in relation to environmental factors such as food and temperature.

Finally, although certain studies of corixid feeding habits have indicated evidence of predation on aquatic invertebrates, many authors state that corixids as a group are primarily microphagous and detritus-feeders. The subject is reviewed below, in Chapter IV. In addition to discussing the feeding pattern, corixid morphology has often been related to possible feeding behaviour, notably by Hale (1922), Hungerford (1919), Jarial et al., (1969), Marks (1957), Parsons (1957b, 1966), Poisson (1923), Slack (1947) and Sutton (1947a, 1951).

Most evidence for competition comes from feeding behaviour. Therefore, the diet of Cenocorixa is likely to show evidence of any competitive displacement or exclusion in the field, in some lakes. Information on feeding in the genus Cenocorixa is given by Jansson (1971) and Jansson and Scudder (1971, 1974), chiefly in the context of successful rearing of both species through several generations on a diet of frozen brine shrimp. There was no direct substantiation of either predation on living prey, or plant feeding, although Scudder and Jansson (1971) speculate that field-collected corixids with red guts may have been feeding on diaptomids.

The present study sought to look further into the conditions of coexistence of the two species of Cenocorixa in a

series of small lakes of differing salinity in central British Columbia. The major study was an investigation of corixid feeding patterns, as these were most likely to provide evidence of competition. Following studies of the environment and of the corixids involved (chapters II and III), experiments feeding different potential prey organisms to corixids under laboratory conditions (chapter IV) were supplemented by gut examination of field-collected corixids from each habitat, using a serological technique to identify the largely fluid gut contents (chapter V). Finally, in the last chapter the data are assessed to see if competitive exclusion provides a plausible explanation of the distribution pattern of _Cenocorixa_ species in the field, in the light of those facets of their biology so far studied.

CHAPTER II. THE ENVIRONMENTAL BACKGROUND

INTRODUCTION : THE STUDY AREA

The main area chosen for study lies in the Fraser Plateau region of central British Columbia and includes lakes that have already been investigated in some detail by Scudder (1969b), Topping (1970) and Cannings (1972). The Becher's Prairie study area is on the Chilcotin Plateau near Riske Creek, west of the Fraser River near Williams Lake. The terrain is gently undulating with a vegetation of <u>Carex</u>, <u>Potentilla</u>, <u>Artemisia</u> and other dry parkland plants (Beil, 1970), interrupted at intervals by belts of Douglas fir, jackpine and aspen, the latter chiefly marking damper areas. Underlying rocks are Permian, Triassic and Tertiary plateau beds. Mean precipitation is 35 cm yr^{-1}, and mean monthly temperatures - 10 C in January and + 25 C in July.

Of about 75 lakes and sloughs on Becher's Prairie, six of the larger were selected for special study, namely Round-up Lake (Phalerope), Lake Lye (Box 20-21), Barnes Lake (Box 4), Lake Greer (Box 89), East Lake (Racetrack) and Rock (Rock) Lake (Names used by Scudder (1969b) in parentheses). These lakes were selected for equivalence of size, permanence and to encompass the salinity range of lakes in the area. There are no permanent inflow or outflow streams linking any of these lakes.

Figure 1 shows something of the morphometry of each lake. The maximum depth of the lakes is about 6 m, although Rock L. and L. Greer are about half this depth. The areas of the

Figure 1. Sketch-map of the study areas, with inserts showing Lake LB 2, and the position of the study areas in B.C.

Lac du Bois

LB 2

Drummond L.

Round-up L.

MILITARY   TRAINING   AREA

B. C.

L. Lye

Barnes L.

Riske, Creek

LB 2

L. Greer

UBC

East L.

Rock L.

RISKE
CREEK

Airstrip

20
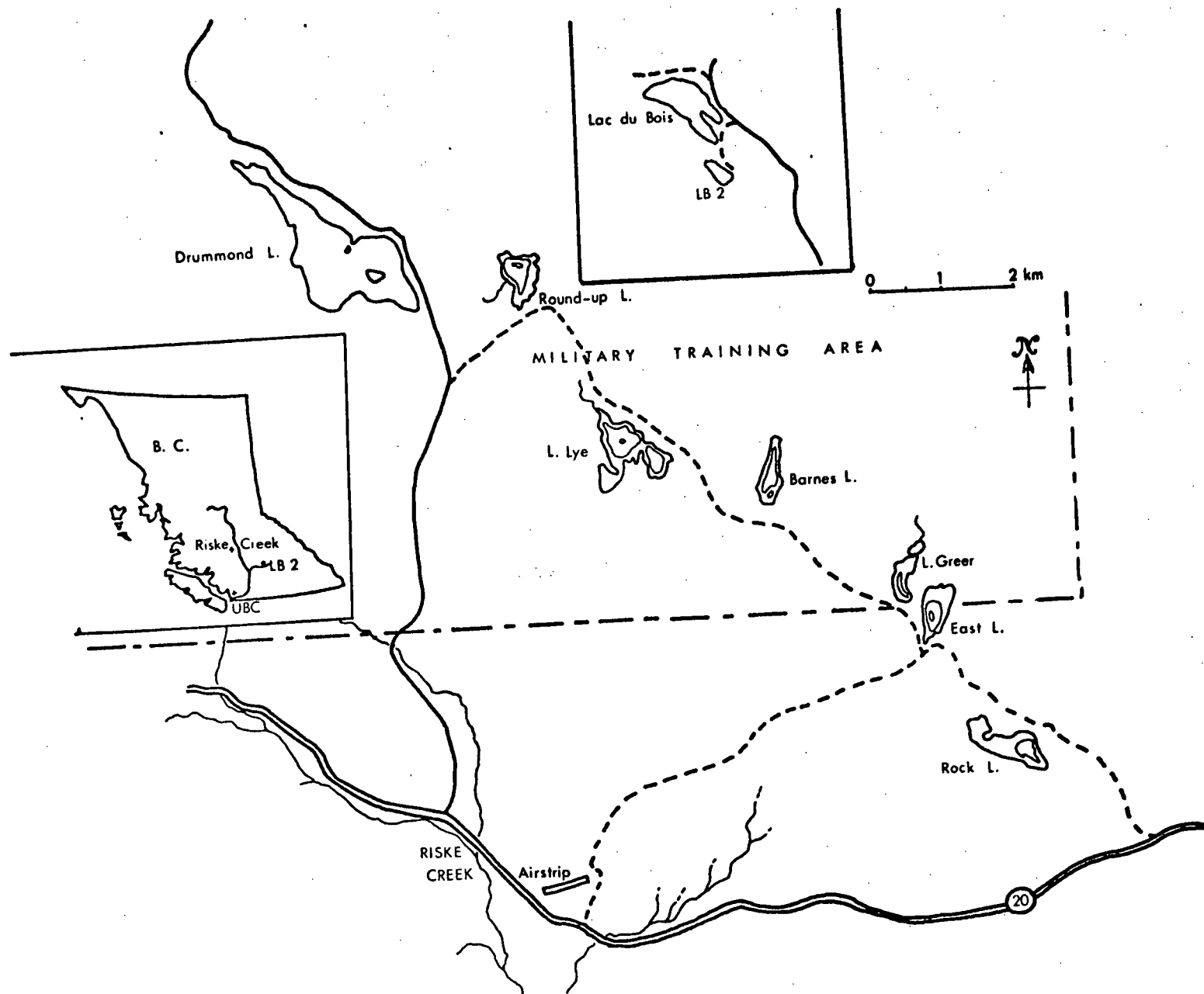
lakes are also fairly similar, and the dominant ions are the same (Table I).

At a similar altitude to the Becher's Prairie lakes (around 900 m), Lake LB 2 (Scudder, 1969), near Lac du Bois in the hills north of Kamloops, was sampled periodically to obtain corixids and potential prey organisms. LB 2 has dimensions similar to the lakes on Becher's Prairie (Table I), and has a mean recorded conductivity of 20,000 μmhos cm^{-1}, with similar dominant ions except for the presence of sulphates.

The morphoedaphic index listed in Table I for each lake was calculated using total dissolved solids measurements (Topping, 1969) and mean depths. This index has proved a useful guide to relative potential production, specifically of fish, of water bodies in restricted areas of similar geography and climate; it was developed from ideas of Northcote and Larkin (1956) and Rawson (1952), and supercedes earlier measures of potential productivity which used depth and area factors (Ryder et al., 1974).

Collections of some potential prey organisms were made at Marion Lake in the U.B.C. Research Forest (Hall and Hyatt, 1974). Samples of corixids and other fauna were also taken in small temporary ponds by Wesbrook Crescent and 16th Avenue on the U.B.C. Endowment Lands in Vancouver.

Lake	Elevation (m)	Area (ha)	Depth (m) Mean	Depth (m) Max.	Conductivity (mhos/cm at 20°C) Range	Conductivity (mhos/cm at 20°C) Mean	pH Range	Major cation	Major anions	Morpho-Edaphic Index
LB 2	899	3.1	1.1	2.5	2720-20580	16514	9.2- 9.7	Na	CO_3, SO_4	15013
Barnes	945	17.2	2.0	4.5	3000-20000	11820	9.3- 9.7	Na	CO_3, HCO_3	4893
Round-up	945	30.8	2.6	6.2	2820- 9000	6890	9.2- 9.3	Na	CO_3, HCO_3	2062
Lye	945	46.5	2.8	5.4	1100-12000	6548	9.1- 9.6	Na	CO_3, HCO_3	1765
Greer	945	15.2	1.0	2.3	1400- 2200	1602	8.4- 9.5	Na	HCO_3	1221
Rock	945	34.6	1.1	2.5	1435- 2600	1496	8.6-10.5	Na	HCO_3	1027
East	945	27.0	1.9	6.5	400- 600	600	7.8- 9.7	Na	HCO_3	196

Table I. Some selected physical and chemical features of the lakes studied (modified in part after Scudder, 1969; Topping, 1969; and Cannings, 1973).

MATERIALS AND METHODS

Since corixids do not feed below 5 C (Jansson and Scudder, 1972) no winter sampling was done. Juveniles of Cenocorixa first appear in the study lakes about mid-May (Jansson and Scudder, 1974). Intensive field sampling was therefore carried out from mid-May to mid-October, 1972, at the Becher's Prairie lakes, and less regularly at Lake LB 2. In both areas, regular samples were also made in 1973. Samples were also collected when necessary at the U.B.C. and Marion Lake sites from 1971 to 1973. The following describes methods and materials for the main study area lakes in the 1972 field studies.

A sampling area was chosen for each lake, reasonably clear of weeds, and as far as possible with similar topography and shore development. The area was sufficiently large to allow sampling all summer with minimal disruption of the habitat. Midlake samples were taken at the deepest points of each lake, as determined from depth charts in Topping (1970).

Limnological Parameters

(i) Temperatures

Surface temperatures were measured at the inshore sampling station over 10 cm of water, and midlake, every four days in each of the six lakes on Becher's Prairie using a Fisher partial immersion thermometer graduated from -10 C to +110 C. Automatic monthly chart recorders (Ryan Model D-30, 0 to +30 C, Chart 380-4) were installed in five of the lakes on Becher's Prairie (except Rock Lake) and recorded temperature from mid-May to mid-October 1972. They were placed in areas of appreciable slope, 1.5 to 2.0 m from shore and 20-30 cm deep; the only marked variable being the presence or absence of weeds.

(ii) Conductivity

Water was collected at approximately monthly intervals from the six Becher's Prairie lakes, filtered through phytoplankton netting (meshes 54µ) and stored in a 1 litre polyethylene bottle for conductivity measurements. Specific conductance was estimated using a Copenhagen Radiometer conductivity meter, type CDM 2d, and results were corrected to a standard 25 C temperature.

Primary Productivity

Three estimations were made of the photosynthetic activity of planktonic algae during the summer of 1972, to obtain an indication of the size of that portion of the algal base of the food web extending eventually to the corixids under investigation.

Water light transmission was measured with a white and black quartered 20 cm diameter Secchi disc. Readings were made every four days at the midlake station in each lake, following Tyler (1968). Weather parameters (wind, degree of cloudiness, precipitation) were recorded on each occasion.

Rodhe (1958) estimated the maximum photosynthetic rate to occur at a level of 20 - 25 percent of total light extinction recorded with a photocell. Since Secchi disc extinction depth represents approximately 15 percent of subsurface illumination measured with a photocell (Steeman Nielsen, 1958) the maximum photosynthetic depth was derived from the simplified photosynthesis-depth and light extinction-depth curves in Vollenweider (1969) to lie at about one third of the Secchi disc extinction depth.

The Miller (1914) method of oxygen determination, elaborated by Walker et al. (1970) was used because of its appropriateness for saline water situations (Thomas, 1953; Bayly and Williams, 1966). Light and dark bottle oxygen changes (described in Patten et al., 1964) were used instead of radio-

isotope tracer techniques (e.g. Steeman Nielsen and Cushing, 1958) after a consideration of field conditions and the experimental situation.

Four cords were attached 40 cm apart to a 2 m long spar with other dimensions 5 by 2.5 cm to hold productivity bottles. These were standard 300 ml reagent bottles (Wheaton No-Sol-Vit No. 2) with ground-glass stoppers; 'dark' bottles and their stoppers were covered in heavy-duty black polythene sheeting secured with black masking tape. Each bottle had a simple cradle of twine leading to a curtain ring; this could be attached to the cord so that the bottle would hang horizontally (Rodhe, 1958) at the desired depth.

At the midlake sampling point the spar was anchored and a Secchi disc transparency reading taken. Four replicate light and one dark bottles were filled, one bottle per litre to allow ample flushing, from a two litre Van Dorn bottle filled 10 cm below the surface. Stoppers were wired in place and black polythene taped over the neck and stopper of the 'dark' bottle as a further precaution against light penetration. Bottles were then hung horizontally at one third of the Secchi disc extinction depth, which approximated the region of maximum photosynthetic rate. The experiment was left to run for six hours from midday, with the spar acting as float and marker but not interfering with light transmission. Midlake water temperature was measured at the start and end of the experiment at the chosen depth. The test period chosen (6 h) was a compromise between inaccuracies in short experiments resulting

from disturbance effects and from delays during titrations, and increasing inaccuracies resulting from longer experiments; these may include depression of photosynthesis (Vollenweider, 1969) and problems of bacterial growth (Steeman Nielsen, 1958).

One dark and three light bottles were used experimentally; the fourth filled bottle was immediately used to obtain initial oxygen readings in the same manner as the others at the end of the experiment. Each bottle was sampled to obtain replicate oxygen determinations, following the Miller method which measures oxidation of ferrous ions in an alkaline medium. A 50 ml sample was placed in a 100 ml conical flask and 5 ml alkaline tartrate reagent plus methylene blue indicator were added. This was titrated with a ferrous solution to the disappearance of the blue colour, using a 20 ml Corning disposable pipette. To minimise addition of atmospheric oxygen the flask was gently swirled and stirred with the submerged tip of the pipette. The titre is approximately equal to the oxygen content in ml, converted to mg l^{-1} by multiplying by 1.43 (Thomas, 1953). If the assumption, not always correct (Bunt, 1965), is made that respiration rates are similar in dark and light, the dark bottle values subtracted from those in the final light bottles give a measure of gross photosynthesis.

Net photosynthesis was obtained by subtracting initial from final light bottle measurements; this, doubled, gives an approximate daily photosynthetic rate at optimum depth (Steeman Nielsen, 1958), which is converted to diel rate by subtracting four times the net respiration rate from the doubled gross

photosynthetic rate. The problems of such conversions from an experimental to a daily rate are stressed by Vollenweider (1969) but remain esentially unsolved. From the information, a Figure for daily primary production was obtained, expressed as mg C fixed per m^2 per day, using 1.9 mg O2 = 1 mg C (Steeman Nielsen and Cushing, 1958).

Aquatic plants

Macrophyte samples were collected monthly, in 1970 by Scudder in all six Becher's Prairie lakes. In 1972 the shoreline of each was traversed monthly and herbarium specimens collected and identified, with a record of abundance, flowering and fruiting status, and position relative to the water's edge, by Sylvia C. P. Reynolds.

Plankton

During 1970 monthly quantitative (2 litre) surface plankton samples were collected inshore in duplicate by Scudder. All those for the six lakes under study were examined and the plankters identified and counted. Diaptomid and cyclopoid copepods were identified following microdissection and mounting in Polyvinyl Lactophenol with lignin pink; most identifications were confirmed by Dr. K. A. Patalas.

In 1972 plankton in all six lakes was sampled quantitatively in duplicate inshore and midlake with a 2-litre Van Dorn water bottle. The collected water sample was filtered through a conical zooplankton net of 417μ mesh size, which retained all adults and a good proportion of nauplii. The outside of the net was washed to concentrate the contents and samples were run into 6 dram glass vials containing about 0.5 dram formaldehyde solution. Any plankters remaining on the net were added using a fine paintbrush. All 2-litre samples were later filtered and the wet volume of plankton measured by displacement to the nearest 0.05 ml. Midlake quantitative samples were supplemented by a vertical haul made with the same net, weighted to allow rapid sinking.

Other Organisms

Semi-quantitative benthic sweep-net samples were collected bi-monthly in 1970 by Scudder and these were examined to obtain some measure of the availability and abundance of potential food organisms. Total displacement volume of whole samples was measured and the volume and total numbers of selected major groups were also determined.

For six weeks from mid-May of 1972 all invertebrates taken in sweep-net samples were preserved; after this date these were not collected quantitatively. Occurrence of certain benthic organisms in 1972 was also obtained from the inshore 2 litre

plankton samples.

RESULTS

Limnological Parameters

(i) Temperatures

Temperature maxima and minima at 30 cm depth read from temperature charts were plotted for each second day for the Becher's Prairie lakes to indicate the extent of daily and seasonal temperature fluctuations (Figure 2). Inshore temperatures were generally higher than those midlake during the day, and in shallower lakes both inshore and midlake temperatures showed more extreme daily fluctuations than in deeper lakes. Mixing seemed to occur throughout the season. In general temperature patterns were similar between lakes, reflecting their proximity and comparable size and depth features.

Following ice-melt about the end of April, 1972, warming was rapid and temperatures reached a fluctuating 'plateau' level by mid-May, when sampling began; this level held until the end of August. Temperatures then fell off slowly but fairly steadily until ice started to form in early October. Maximum recorded temperatures for 1972 were similar in all lakes, the highest being 26.7 C for Round-up Lake in August. The temperature data

Figure 2. Daily temperature ranges in five Becher's Prairie lakes, recorded at two day intervals from May to October, 1972.

20° —

Barnes

0 — M | J | J | A | S | O

20° —

Round-up

0 —

20° —

Lye

0 . —

20° —

Greer

0 —

20° —

East

0 — MAY | | | | | OCT.
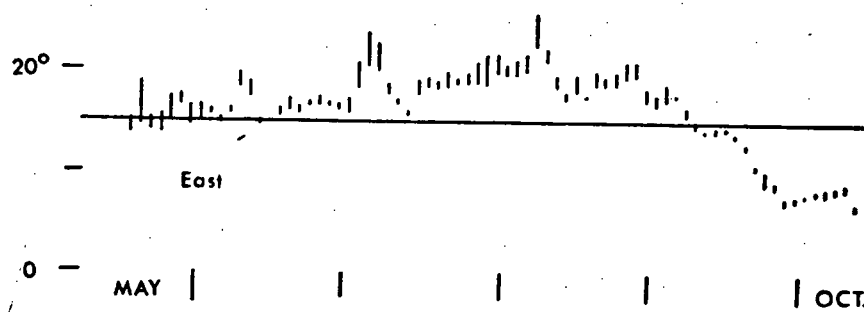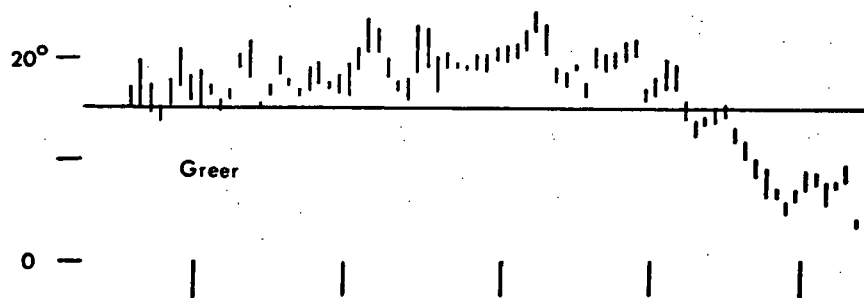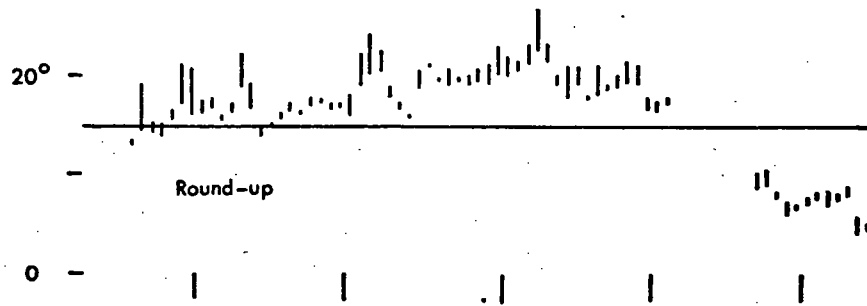
indicate that in 1972 this parameter remained similar to that recorded in previous seasons (Cannings, 1973; Jansscn and Scudder, 1974).

(ii) Conductivity

Conductivity was measured on four occasions during 1972. Conductivities increased as the season progressed, reaching highest levels in October; this was due chiefly to the gradual mixing of a surface layer of low-salinity meltwater with deeper, more saline waters. The conductivity values recorded (Figure 3) fall consistently around the high end of the ranges given by Scudder (1969b), indicating no significant departure from the previous conditions recorded in these water bodies.

Primary Productivity

Oxygen determinations and preliminary productivity estimates indicate that in the three more freshwater lakes on Becher's Prairie oxygen levels were generally higher than in the more alkaline waters and production by phytoplankton was at times high (Table II). However, the data also suggest that production by planktonic algae is not important in replenishing water oxygen in the three most alkaline lakes. In fall production was low, even in the more freshwater lakes.

Secchi disc water transparency data collected tc assess

Figure 3. Range of conductivities measured in seven study lakes in 1972. Vertical bars indicate ranges recorded in the literature.
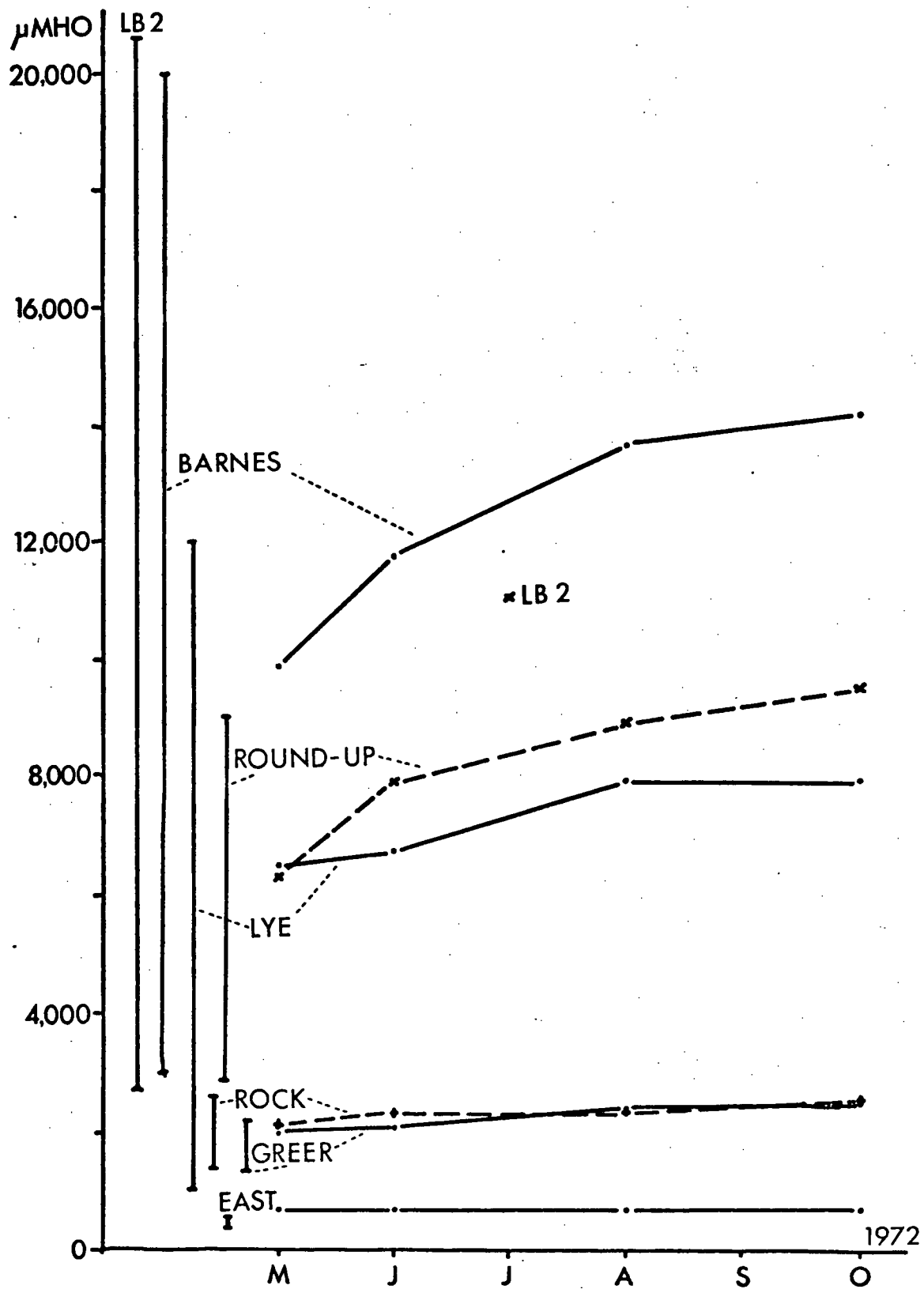
Table II. Primary production estimates and surface oxygen readings in six lakes on Becher's Prairie (For details of calculations see text).

LAKE	PARAMETER	18 MAY	27-31 MAY	7-9 AUG	20-21 SEP
Barnes	depth[1]	10	50	53	63
	temp[2]	16.0	18.5	24.4	10.0
	oxygen[3]	9.15	7.15	6.68	8.44
	photosyn[4]		0.50	-1.28	0.36
	productn[5]		95	neg.	68
Round-up	depth[1]	10	50	55	
	temp[2]	11.6	17.6	24.0	
	oxygen[3]	9.65	7.51	7.05	
	photosyn[4]		(-1.48)	1.24	
	productn[5]		neg.	236	
Lye	depth[1]	10	60	73	70
	temp[2]	12.1	17.2	23.2	11.0
	oxygen[3]	8.91	7.87	6.86	8.58
	photosyn[4]		2.22	2.14	0.92
	productn[5]		422	407	175
Greer	depth[1]	10	30	65	57
	temp[2]	14.0	20.8	24.5	9.6
	oxygen[3]	10.01	14.47	6.44	8.44
	photosyn[4]		9.18	0.64	1.04
	productn[5]		1744	121	198
Rock	depth[1]	10		38	
	temp[2]	14.5		23.4	
	oxygen[3]	11.08		8.39	
	photosyn[4]			0.26	
	productn[5]			49	
East	depth[1]	10	10	28	26
	temp[2]	14.0	19.5	27.4	10.9
	oxygen[3]	10.08	22.52	13.59	5.62
	photosyn[4]		2.36	4.72	0.72
	productn[5]		448	897	137

[1] : test depth (cm)
[2] : temperature (C)
[3] : surface oxygen (mg l^{-1})
[4] : net diel photosynthesis (mg l^{-1})
[5] : primary production (mg C m^2 24h).

light penetration in conjunction with the plankton and productivity study are recorded, with observations of algal blooms, in Figure 4. Marked fluctuations in transparency were noted and no doubt relate to blooms, to atmospheric conditions and to silt washed in after heavy rains. There was no consistent pattern across the lakes, although in some, transparency declined in fall.

Aquatic Macrophytes

Although one species of Najadaceae occurred in quantity in Lake LB 2 which has a mean conductivity of 20,000 μmhos cm^{-1}, no plants were found in the three most alkaline lakes on Becher's Prairie. However, in the other lakes (conductivity below 2,600 μmhos cm^{-1}) Myriophyllum and najadaceous plants were often abundant (Table III) and formed extensive inshore fringes up to a depth of about 1.5 m. Macrophyte growth was rapid once warming of the lakes started, forming meadows by the end of May, with distinct zonation with depth. Fringing bands usually had Zanichellia inshore, then Potamogeton, Myriophyllum and finally Ruppia in the deepest water. Plants started to die back in early September as temperatures fell, and by the approach of freeze-up most macrophytes had again disappeared.

Juncus and Scirpus species grew on the damp shorelines of all lakes, occasionally entering the water in the three most alkaline lakes and in Rock Lake. They thus provided almost the

Figure 4. Secchi disc water transparency in six Becher's Prairie lakes, measured at 4 day intervals in 1972. Shaded areas ('b') indicate presence of strong algal blooms.
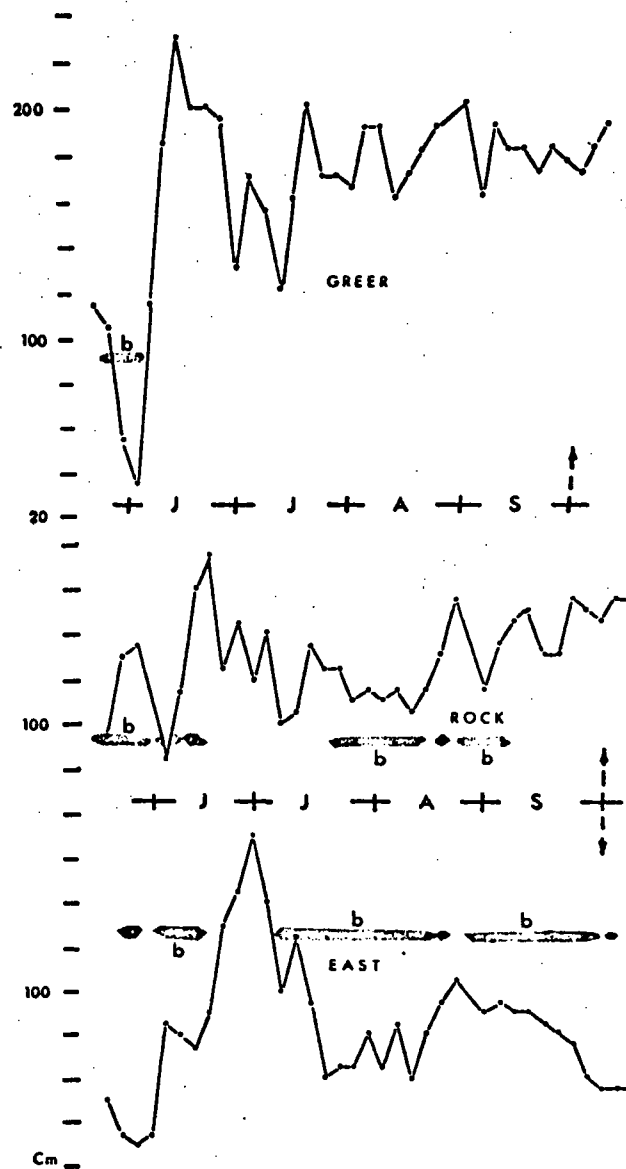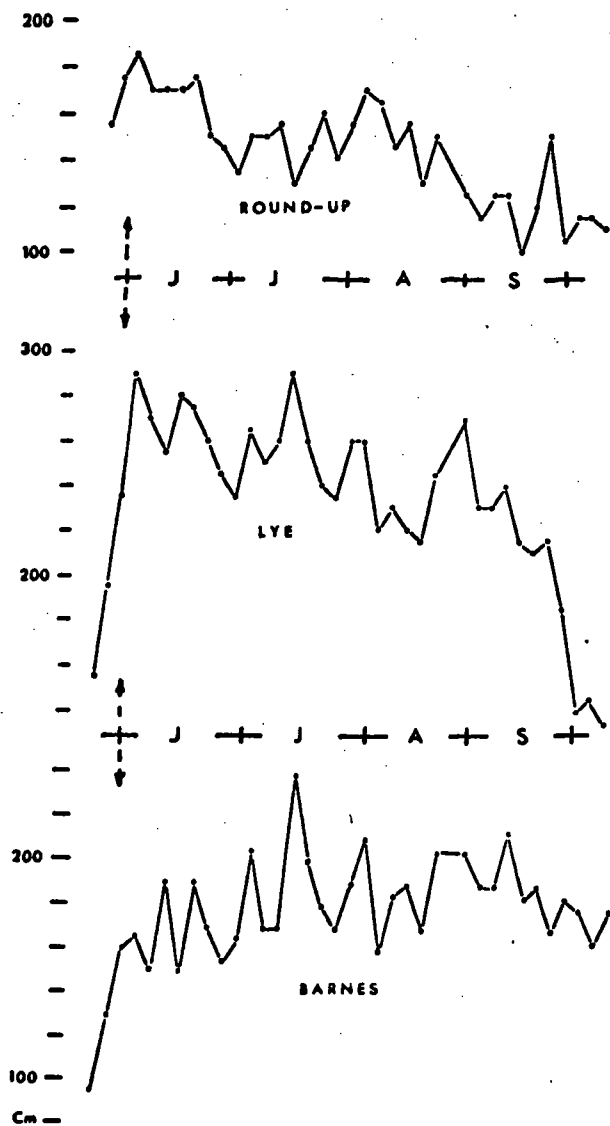
Table III. Distribution of aquatic macrophytes cf the Becher's Prairie lakes and Lake LB 2.

	LB 2	Barnes	Round.	Lye	Greer	Rock	East
EMERGENTS :							
Scirpus validus		x	x	x	x	x	
Juncus balticus	x	x	x	x	x	x	x
Carex species		x	x				
SUBMERGED:							
Myriophyllum spicatum					x	x	x
Ceratophyllum demersum							x
Potamogeton pectinatus					x	x	x
P. pusillus or foliosus							x
Potamogeton species	x						
Ruppia maritima					x	x	
Zannichellia palustris					x	x	
Polygonum amphibium					x		x

only cover for organisms in Barnes and Round-up Lake and Lake Lye.

Plankton

Although the plankton determinations were chiefly made from 1970 samples, vertical haul samples from 1972 indicated a similar distribution of species in the lakes studied. Thus, plankton data for 1970 could be used to supplement 1972 information.

Diaptomid copepods were present only in the three most alkaline lakes on Becher's Prairie and in LB 2; none were ever recorded from the three fresher water lakes (Table IV). Cyclopoid copepods and daphniids were found in all lakes, but the species composition varied with alkalinity. Some species were found in all or almost all lakes, while others appear to have quite a restricted distribution. In Lakes LB 2 and Barnes large zooplankton species such as _Diaptomus nevadensis_ and _Daphnia_ spp. were less apparent than in other lakes, the plankton being dominated by small diaptomid species and by ceriodaphniids. This pattern is seen in the absence of fish or other vertebrate predators in these lakes.

Mean volumes of plankters over the summer of 1972 are shown in Figure 5, and seasonal means for midlake and inshore samples are listed in Table V. Inshore values were always higher than those obtained for midlake samples. The magnitude of the mean

Table IV. Occurrence of zooplanktonic crustaceans in the study lakes. Parentheses indicate either a single observation, or literature references not authenticated in this study.

	LB 2	Barnes	Round	Lye	Greer	Rock	East
Plankters :							
Diaptomus sicilis	x	x	x	x			
D. nevadensis		(x)	x	x			
Eucyclops agilis			x	x	x		x
Cyclops vernalis				x	x	x	x
C. navus					x		
Cyclops sp.		x					
Paracyclops fimbriatus						x	
Macrocyclops albidus							x
Daphnia pulex		x	x	x	x	x	x
D. similis		x	x	x	x	x	
D. schodleri		x	x	x	x	x	x
D. magna						x	x
Ceriodaphnia quadrangulata				x	x		
C. reticulata							x
Ceriodaphnia species		x				x	
Moina hutchinsoni		x					
Moina rectirostris			x				
Simocephalus vetulus			x		x	x	x
Scapholeberis kingii					x	x	x
Chydorus sphaericus							x
Number of plankter taxa	1	7	8	8	9	9	10

Figure 5. Plankton volumes (ml l^{-1})in replicated inshore 2 litre samples taken at 4 day intervals in the Becher's Prairie lakes in 1972.
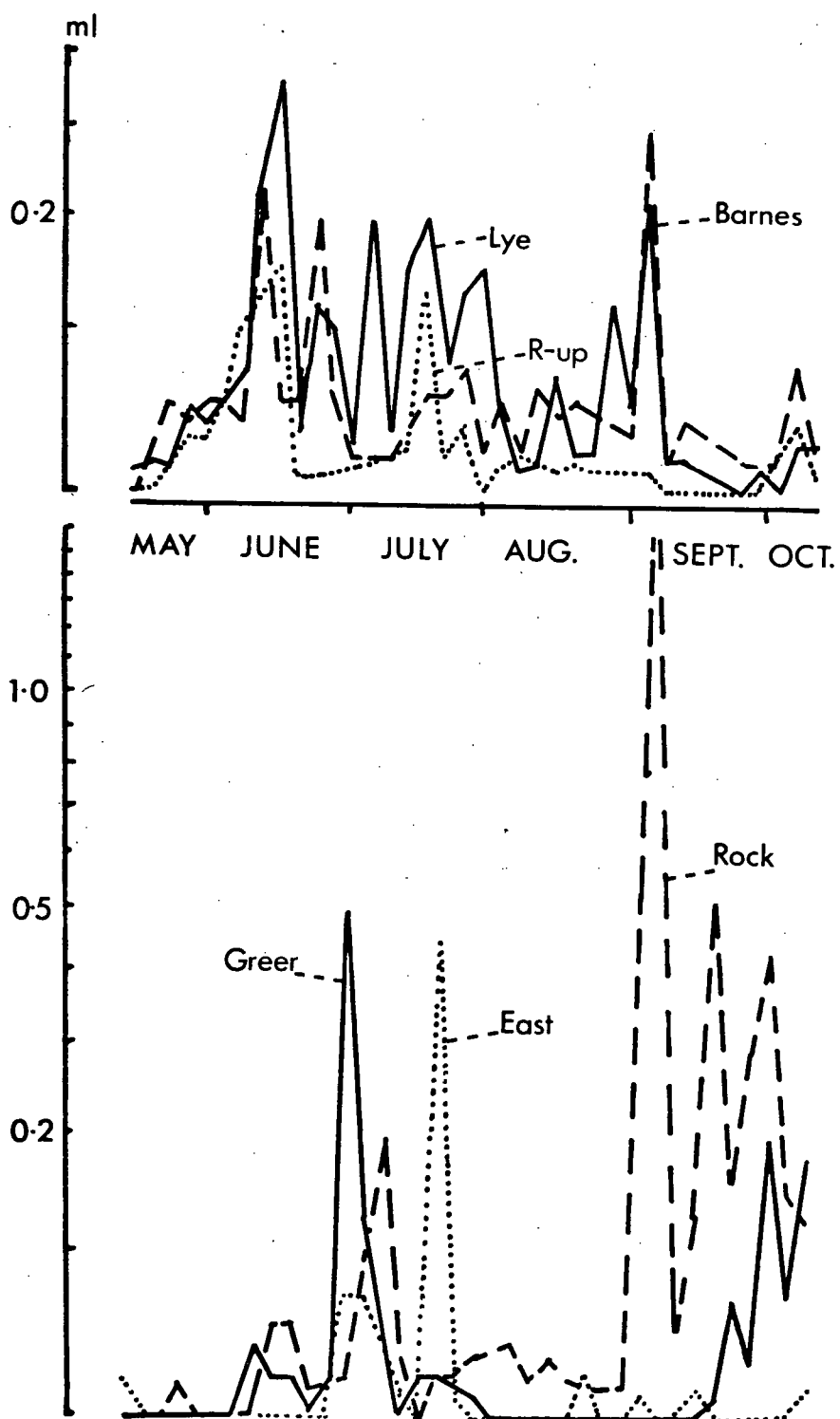
Table V. Seasonal means of plankton volumes in ml.l⁻¹, from duplicate 2 litre samples collected at 4-day intervals.

LAKE	INSHORE :	MIDLAKE :	RATIO IN:MID :
ROCK	0.1218 (37)	0.0036 (34)	33.8:1.0
LYE	0.0379 (36)	0.0054 (33)	7.0:1.0
BARNES	0.0290 (38)	0.0063 (35)	4.6:1.0
GREER	0.0202 (38)	0.0033 (36)	6.1:1.0
ROUND-UP	0.0182 (35)	0.0042 (34)	4.3:1.0
EAST	0.0113 (37)	0.0036 (35)	3.1:1.0

seasonal difference ranged from 3.1 to 7.0 times more inshore than midlake, with an extreme value of 33.8 times more inshore than midlake in Rock Lake.

Inshore plankton in the three more alkaline lakes rarely fell below 0.1 ml per 2 litre sample. However in the more freshwater lakes, inshore plankton was in general very scarce in May and early June, and again in August and the first half of September, and was abundant in the littoral of these lakes only from mid-June to August.

Moinids (in Barnes Lake) and daphniids peaked early in the alkaline lakes in 1970, then decreased as diaptomids rose (Figure 6). The daphniid peak in the more freshwater lakes occurred contemporaneously with that for diaptomids in the more saline lakes. Cyclopoid copepods dominated the plankton in the freshwater lakes in spring, before daphniid populations had become well established.

Overall, plankton abundance was at a fairly high level in all lakes, with a spring dominance of diaptomids in the more alkaline lakes and a high population of daphniid plankters in the littoral of the freshwater lakes in midsummer and again in late fall.

Figure 6. Numbers of some plankters per 2 litres at different times of year in lakes on Becher's Prairie, from 1970 samples. Graph points represent monthly samples, May to September.

A: All _Daphnia_ species.   a: Greer, b: East, c: Lye Lakes.

B: Diaptomids and _Moina_.

    D. sicilis; a: L. Lye, b: Round-up, c: Barnes L.

    Moina sp.;   d: Barnes L.

C: Cyclopoids.   a: Rock, b: Greer, c: East, d: Lye Lakes.
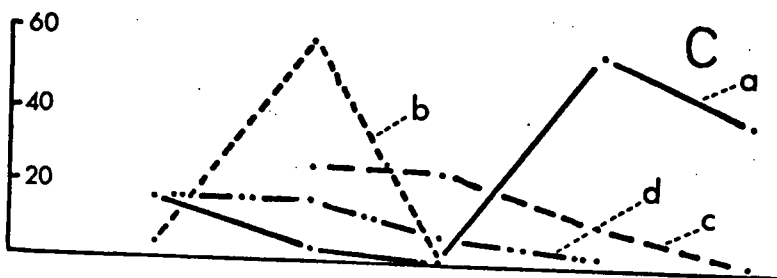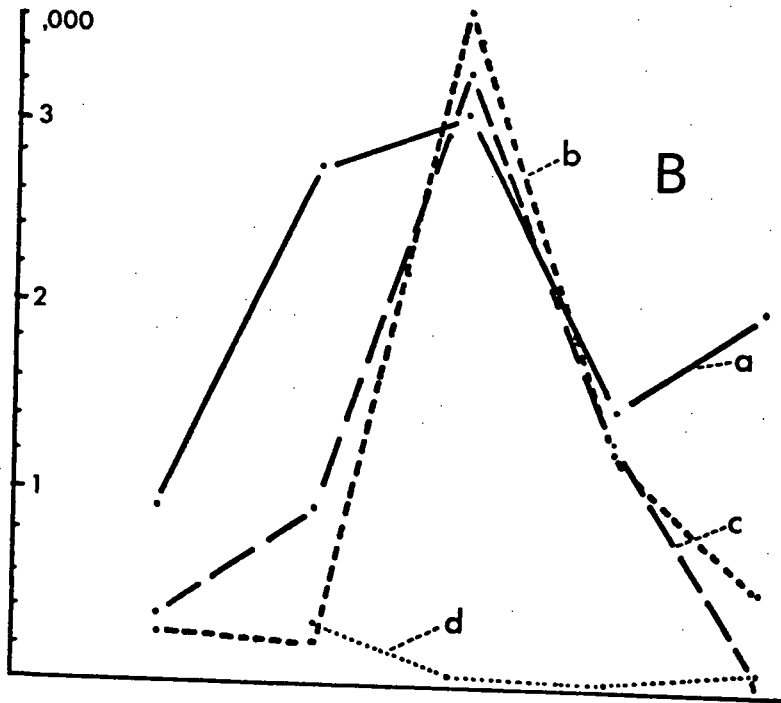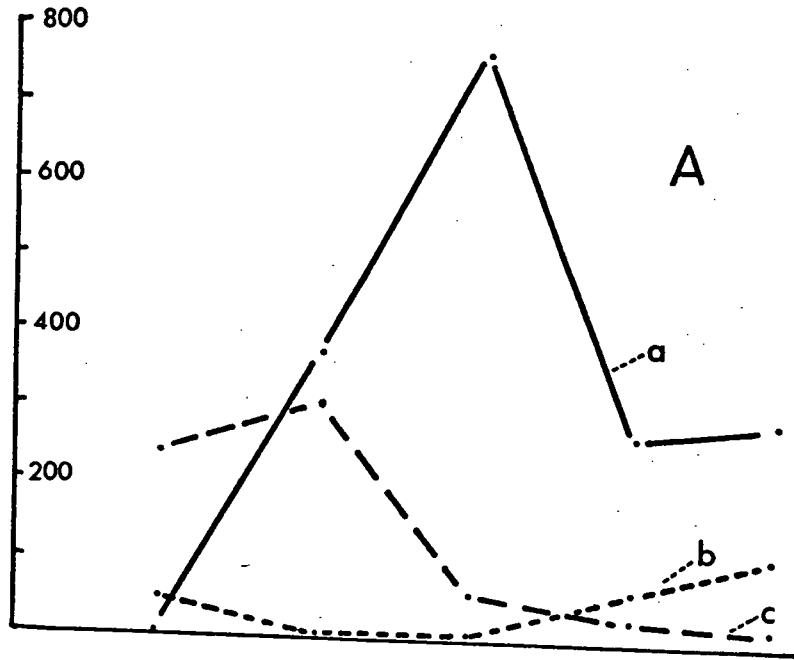
Other Organisms

Table VI lists the occurrence of the major benthic faunal components in each lake, from sweep-net samplings and literature records (Scudder, 1969b; Topping, 1968; Cannings, 1973). While few macroscopic organisms were seen in Lake LE 2, there is a wide range of forms present in the other lakes; a few taxa such as Chaoborus and amphipods are confined to the freshwater lakes, and fairy shrimps (Branchinecta) to the most alkaline waters.

Data from 2 litre plankton and sweep-net samples plotted at four day intervals (Figure 7) show that chironomid and coleopteran larvae and zygopteran and ephemeropteran naiads are present in all lakes over most of the summer. Zygopteran nymphs occurred in all lakes, but most abundantly among submerged plants. Young nymphs were conspicuous in the littoral fauna over most of the summer. Ephemeropteran nymphs were also common all year, with small forms seen chiefly after mid-summer.

Chironomid larvae were present in all lakes in the mud and among weeds, emerging at different times throughout the summer season (Cannings, 1973). Sweep-netting and plankton sampling greatly underestimated their biomass, as only individuals in the water column were captured, so data from Cannings (1973 and unpublished) have been presented as Table VII.

In the freshwater lakes chaoborid larvae and amphipods were also present throughout the year. Branchinecta were abundant in Lake LB 2 throughout the summer, but were seen only vernally and

Table VI. Occurrence of major constituents of the invertebrate fauna in the lakes studied. Parentheses indicate either a single observation, or literature references not authenticated in this study.

	LB 2	Barnes	Round.	Lye	Greer	Rock	East
ORGANISMS :							
Chaoborus l.			(x)		x	x	x
Aedes l.		x	x	x	x	x	x
Chironomid l.	x	x	x	x	x	x	x
Nctonecta sp.		x	x	x	x	x	x
Enallagma sp.		x	x	x	x	x	x
Callibaetis sp.		X	x	x	x	x	x
Trichoptera l.		x	x	x			x
Coleoptera	x	x	x	x	x	x	x
Hydracarina		x	x	x	x	x	x
Ostracoda					x	x	
Branchinecta sp.	x	x	x	x			
Amphipoda			(x)	(x)	x	x	x
Snails							x
Leeches					x	x	x
Number of groups	3	9	10	10	11	11	12

Figure 7. Spatial and temporal distribution of major invertebrates in six Becher's Prairie lakes sampled by sweep-net at 4 day intervals in 1972.

1= Barnes, 2= Lye, 3= Round-up, 4= Greer, 5= Rock, 6= East Lakes.

A= chironomids, B= chaoborids, C= zygopterans, D= ephemeropterans, E= amphipods, F= beetle larvae.

May   June   July   August   September   Oct.
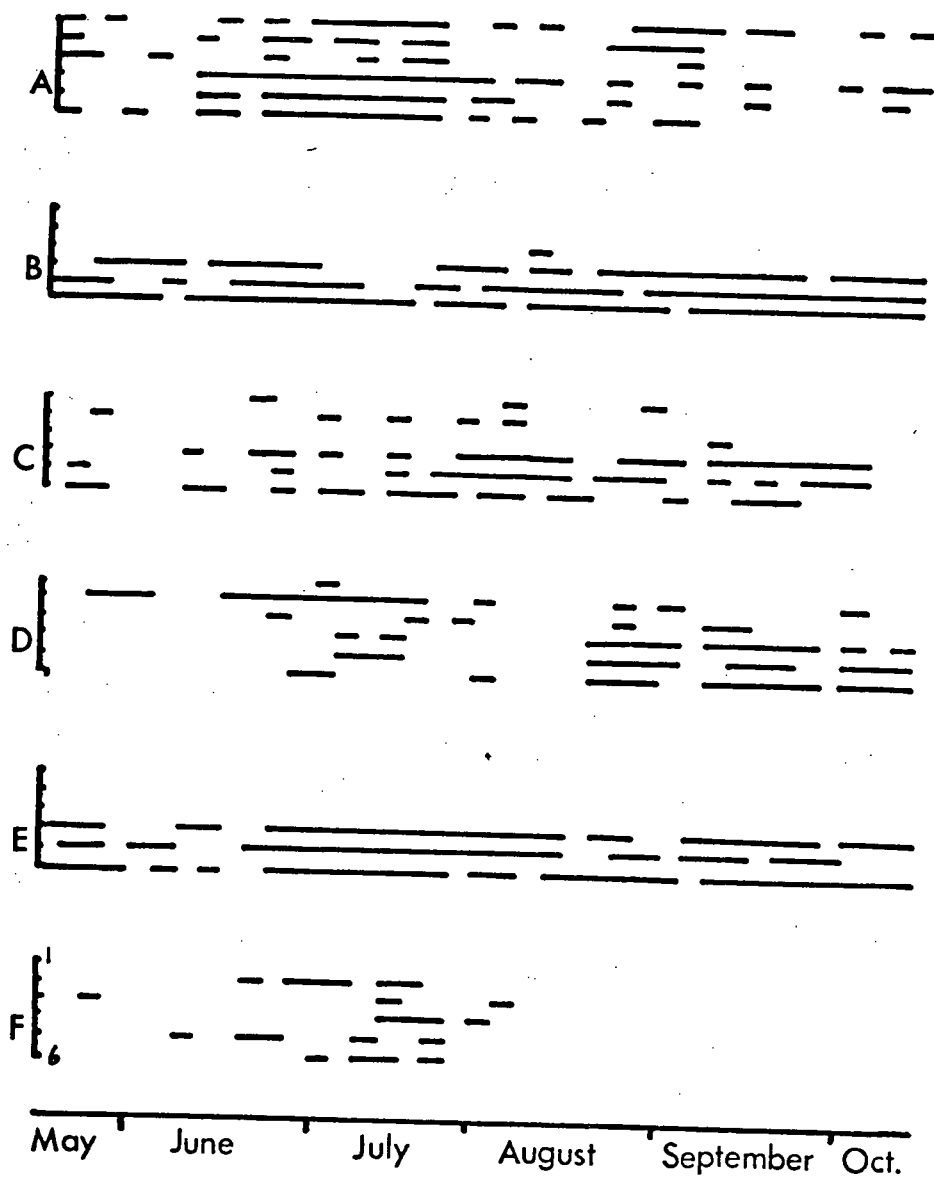
Table VII. Chironomid larval abundance and biomass in six Becher's Prairie lakes (after Cannings, 1973 and unpublished data)

LAKE	Larval biomass (ml per m²)	Maximum numbers per m² (May-Oct) (means of 2 samples)	Minimum numbers per m² (May-Oct)
BARNES	21.0	11631 (Aug)	774 (June)
ROUND-UP	1.5	3827 (July)	150 (June)
LYE	10.0	2515 (Aug)	150 (June)
GREER	40.0	14188 (Aug)	3311 (May)
ROCK	20.0	72706 (Aug)	537 (May)
EAST	35.0	14104 (July)	2128 (May)

in small numbers on Becher's Prairie, being absent from Lakes Lye and Round-up after the end of May, and from Barnes Lake, where they were rather more frequent, by the end of the first week in June, 1972; a pattern also followed in other years.

Relative abundance of the major invertebrate forms was assessed from Scudder's semi-quantitative standard sweep-net samples for June, August and October, 1970. Volume of benthic faunal elements, as a measure of biomass, shows that this was greatest in East Lake and in Lake Greer (Table VIII). According to Cannings (1973) chironomid larval biomass ranged up to 40 cm^3 larvae per m^2 of mud surface at a depth of one m (Table VII), and numbers in excess of 40,000 larvae per square metre were recorded for one species alone in the more freshwater lakes.

The 1970 plankton information paralleled data for 1972 and show an early dominance of plankters in the littoral fauna in the more alkaline lakes, in contrast to their relative paucity at first in the more freshwater lakes. Nevertheless, there was a considerable biomass of organisms present in all lakes at all times, although the species composition varied, being more diverse in the freshwater lakes. The biomass of organisms was consistently highest in the more freshwater lakes, with amphipods the main consituents. In the more alkaline lakes the benthic fauna was rather poorer than in the freshwater lakes, but there was abundant planktonic life, particularly diaptomids, all year.

Faunal group: Lake		ZYGOPTERANS Jun.	Aug.	Oct.	EPHEMEROPTERANS Jun.	Aug.	Oct.	CHIRONOMIDS Jun.	Aug.	Oct.	CHAOBORIDS Jun.	Aug.	Oct.	COLEOPTERANS Jun.	Aug.	Oct.
BARNES	% volume	4.7	-	-	-	-	-	1.2	9.1	16.7	-	-	-	-	-	-
	Number	17	-	-	-	-	-	63	2	48	-	-	-	-	-	-
ROUND-UP	% volume	-	+	-	+	-	14.3	10.0	-	28.6	-	-	-	-	-	-
	Number	-	1	-	2	-	3	5	-	41	-	-	-	-	-	-
LYE	% volume	1.0	-		1.0	0.9		1.0	+		-	-		1.3	-	
	Number	10	-		26	1		62	10		-	-		27	-	
GREER	% volume	0.9	3.9	0.4	-	+	7.0	0.9	+	+	8.1	+	+	0.9	+	-
	Number	9	143	30	-	16	761	17	19	8	103	6	2	4	6	-
ROCK	% volume	4.7	8.3	-	-	8.3	+	-	0.9	+	2.8	+	+	-	1.7	-
	Number	5	112	-	-	28	7	-	18	10	17	4	2	-	6	-
EAST	% volume	8.9	2.1	3.2	-	0.7	2.0	+	+	-	47.9	+	0.6	+	0.5	-
	Number	48	248	98	-	72	544	2	46	-	944	2	68	1	2	-

	TRICHOPTERANS Jun.	Aug.	Oct.	AMPHIPODS Jun.	Aug.	Oct.	CORIXIDS Jun.	Aug.	Oct.	PLANKTON Jun.	Aug.	Oct.	OTHERS		TOTAL VOLUME (ml) Jun.	Aug.	Oct.
-	-	-	-	-	-	10.5	90.9	33.3	83.7	-	50.0	-	All	4.3	1.1	0.3	
-	-	-	-	-	-	163	348	19					Excluding plankton	0.7	1.1	0.2	
10.0	1.6	28.5	+	-	-	10.0	16.7	-	70.0	81.7	28.6	-	All	0.5	3.0	0.4	
7	2	5	1	-	-	11	209	-					Excluding plankton	0.2	0.6	0.3	
1.1	0.1		-	-		3.4	56.6		91.2	41.5		-	All	29.6	5.3		
12	1		-	-		60	281						Excluding plankton	2.6	3.1		
-	-	-	62.4	81.1	42.0	5.1	7.9	1.2	18.8	5.9	48.0	Notonectids Leeches Hydracarina	All	11.7	25.4	25.0	
-	-	-	425	2800	1737	68	206	17					Excluding plankton	9.5	23.8	13.0	
-	-	-	43.4	37.5	1.0	1.0	12.5	0.2	47.2	30.9	98.2	Hydracarina	All	5.3	12.0	19.9	
-	-	-	156	472	17	9	110	1					Excluding plankton	2.8	8.3	0.4	
-	-	-	34.2	23.7	17.6	+	2.1	0.6	4.1	65.3	75.9	Notonectids Leeches Snails Hydracarina	All	14.6	97.0	99.4	
-	-	-	182	2378	1806	10	110	34					Excluding plankton	14.0	31.7	24.0	

Table VIII. Volumetric abundance data for major faunal components of sweep-net samples in six lakes.

DISCUSSION AND SUMMARY OF FINDINGS

The Becher's Prairie lakes lie at a latitude of 52° 0' N whereas Lake LB 2 lies at latitude 50 45' N and at a slightly lower altitude. Lake LB 2 thus has, as a result, a shorter photoperiod but slightly warmer water in the April to November ice-free period (Jansson and Scudder, 1974), both cf which might affect generation success cf aquatic invertebrates.

The temperature and conductivity data indicate that the major physico-chemical conditions in the Becher's Prairie lakes in 1972 fell generally within the ranges encountered in the ten years of previous study. It was therefore concluded that 1972 was not an atypical year and data from 1972 could be usefully compared with data obtained by previous workers.

Among the lakes studied, the chief differences were seen in conductivity. This determines, directly or indirectly, many of the biological parameters of lakes, influencing faunal composition and the presence or absence of aquatic macrophytes. The results of investigations on macrophytes, productivity, zooplankton and macroscopic organisms show clearly that the lakes studied are quite diverse and undoubtedly the differing conditions impose certain limitations on the Corixidae able to exist in these water bodies. Table IX summarises the contrasting conditions in the Becher's Prairie lakes studied.

In general, the distribution of macrophytes would seem to provide extensive inshore areas for macrofaunal congregation in

Table IX. Summary of the distribution patterns of contrasting conditions in the study lakes.

	LB 2	BARNES	ROUND.	LYE	GREER	ROCK	EAST
Macrophytes	x				x	x	x
Primary Production		low	low	low	high	high	high
Chaoborus sp.					x	x	x
Amphipods					x	x	x
Branchinecta sp.	x	x	x	x			
Diaptomus sp.	x	x	x	x			
Plankton abundance		all year	all year	all year	summer fall	summer fall	summer fall

the more freshwater lakes. Further, the structural heterogeneity introduced by plant stands should result in many diverse and discrete habitats there. The absence of macrophytes from the more alkaline lakes on Becher's Prairie might impose severe limitations on the macrofauna in them; certainly without plants the habitat is less diverse.

The Miller oxygen determination method has recently been shown to be highly dependent upon pH, and therefore to need frequent standardisation of the sodium potassium tartrate reagent (Ellis and Kanamora, 1973). Thus, results presented here may be less accurate than was hoped, but give a general picture of relative levels of productivity at different times; this is all that the productivity data aimed to do.

With these limitations in mind, the results indicate a moderate level of production in the more alkaline lakes and a higher one in the freshwater lakes. There was a strong decrease in production levels in September. The latter may partly be a function of overcast skies (Rodhe, 1958), lowered temperatures and reduced algal blooms, but may also be owing to the relatively low angle of the sun; in Alaska Dugdale and Wallace (1960) attributed zero or negative results after mid-July to this factor. In the three most alkaline lakes algae were seen in vertical hauls towards the end of summer, but not in large quantities, and periphytic or epipelic algal development was similarly restrained.

Talling et al. (1973) obtained a photosynthetic level close to the theoretical upper limit by blue-green algae in soda

lakes, and Talling (1970) shows that, as a broad generalisation, heavier phytoplankton standing crops may be maintained in more strongly buffered alkaline waters, and it is likely that all Becher's Prairie lakes fall into the high-alkaline category in this respect. However, standing crop data should not be regarded as synonymous with production data. Parsons et al. (1972) indicate that standing crop may be a misleading guide to algal production, for fertilisation of Great Central Lake on Vancouver Island, B.C. led to little change in algal standing crop, but doubled eutrophic zone productivity: the potential algal increases were largely removed by increased grazing of zooplankters (LeBrasseur and Kennedy, 1972). Thus, despite the restrained algal development and lack of macrophytes in the three most alkaline lakes, there is probably heavy and sustained phytoplankton production since there is a constantly large herbivorous plankton population present in these water bodies.

No work was done on the relative contribution of plants other than planktonic algae to production. However, much of the production in the more freshwater lakes may come from submerged macrophytes and their associated filamentous green algae, and in the more alkaline lakes, a proportion of production may be derived from epipelic blue-green algae.

Most taxa of littoral invertebrates of possible importance as corixid food were represented through much of the salinity range studied. However, _Chaoborus_ and amphipods were apparently excluded from highest salinities, while _Branchinecta_ was confined to these. The number of conspicuous groups decreased

with increasing alkalinity, a feature seen also for planktonic crustaceans and aquatic macrophytes. In particular, Chironomidae, Zygoptera and Ephemeroptera were rather more abundant in the low salinity lakes, a feature perhaps related to the greater degree of protection and camouflage afforded by the dense inshore vegetation.

The zooplankton was sharply different in composition between lakes. In the higher salinity lakes the plankton was characterised by one to two species of Diaptomus; these were frequent or abundant throughout the growing season, and peaked in June to July (Figure 6). In the more freshwater lakes Diaptomus was absent. In such lakes zooplankton populations were low in spring, consisting chiefly of small cyclopcid copepods; daphniids were almost absent until mid-June, but formed swarms in midsummer and again in late fall, for very restricted periods of time. In the freshwater lakes in particular, plankton was most abundant in the inshore areas.

Apart from plankters, the biomass of the freshwater lake invertebrates was consistently higher than that of the more alkaline water bodies. The bulk of this biomass was composed of amphipods, but diversity of invertebrate taxa was also highest in these lakes.

Following studies of Rawson and Moore (1944) on saline lakes in Saskatchewan, Jansson (1971) assumed that conductivity was correlated positively with productivity rates in the saline lakes of central British Columbia. The present studies show that productivity by phytoplankton is apparently greater in the less

alkaline lakes. Secondary production appears to follow a similar pattern. Nevertheless there seems to be ample abundance of food in all lakes, with a potentially wider choice of foodstuffs in the more freshwater lakes.

If the corixid species are general feeders, then food limitations would appear not to be a factor of major importance in their distribution and coexistence. However, should the different species of Corixidae prove to have limited food preferences either all year, or seasonally, then the field data suggest that severely limiting situations might exist in certain lakes.

CHAPTER III. THE CORIXIDAE

INTRODUCTION

In 1972 studies on the distribution, abundance and phenology of corixid species in the lakes of Becher's Prairie were carried out to confirm baseline data obtained by Scudder (1969a) and Jansson and Scudder (1974). These data were not only necessary for a measure of any competitive interaction, but were important in a detailed consideration of the feeding patterns of the species. Further studies were made in the three most alkaline lakes in 1972 and 1973 to investigate possible differences in abundance of the two species of _Cenocorixa_ in different habitats, for such habitat preferences could lessen direct competition.

MATERIALS AND METHODS

Every four days, corixid samples were collected in each of the six Becher's Prairie lakes, using a 'standard sweep' covering approximately 1 m of bottom, forewards and backwards (Jansson, 1971) and taking about one second per movement. A 20 cm diameter round-mouthed net (Freshwater Biological Association, Windermere, England) was used, with mesh size sufficiently small to retain all corixid instars.

Depending on corixid density three, five or ten sweeps were made at a pre-selected station in 10 to 40 cm of water.

Collection areas in each lake were as similar as possible, with gently sloping silt or mud shores, usually with occasional rocks or logs. Aquatic plants were unavoidably present in the three lakes of lowest alkalinity (Greer, East and Rock Lakes).

On five occasions more intensive sampling was used to investigate different habitats within a lake. Several replicate sweeps were collected both inshore and offshore at gravelly, muddy and reedy areas, to obtain around 100 adults and larger juveniles at each. Sweep-net efficiency was lowered in deeper waters, as drag reduced sweeping speed, and as the depth provided a clear escape area above the net.

Corixids were collected and preserved in 75% ethanol, then counted and identified in the laboratory, using the keys of Hungerford (1948), Cobben and Pillot (1960), Scudder (1966) and Jansson (1972a).

RESULTS

Corixid Distribution and Abundance

The occurrence of all corixid species in the lakes studied is summarised in table X. The findings corroborate the data in Scudder (1969a) and show some extension of the casual ranges of four species in the higher alkalinity lakes. It is seen that Cenocorixa bifida hungerfordi Lansbury occurred in all lakes

Table X. Summary of the distribution patterns of corixids in the studied lakes. b represents breeding population; parentheses indicate records from Scudder (1969) but not authenticated in the present study.

	LB 2	BARNES	ROUND.	IYE	GREEN	ROCK	EAST
Cenocorixa bifida	b (x)	b x	b x	b x	b x	b x	b x
Cenocorixa expleta	b x	b x	b x	b x			
Cymatia americana		x	x		b x	b x	b x
Hesperocorixa laevigata		x	x	x	b x	b x	b x
Callicorixa audeni			x	·x	x	b x	b x
Sigara sp.				x	b x	b x	b x
Dasycorixa rawsoni		(x)	(x)	(x)			

investigated, and, in the high salinity lakes Barnes, Lye and Round-up coexisted with <u>Cenocorixa</u> <u>expleta</u> (Uhler); the latter was never captured in the three freshwater lakes. Other species of Corixidae occurred sporadically in the lakes, but only in the three freshwater lakes can these forms be considered as permanent residents with breeding populations.

The temporal sequence of the instars and generations in <u>C</u>. <u>bifida</u> and <u>C</u>. <u>expleta</u> in the Becher's Prairie lakes studied is shown in figure 8. The results show a close correspondence with those of Jansson and Scudder (1974). Breeding ended earlier in the more freshwater lakes. <u>C</u>. <u>expleta</u> showed a third generation in Barnes Lake, the most alkaline water body, but indications of this were slight in Lake Lye, while in Round-up Lake only two clear generations were produced. <u>C</u>. <u>bifida</u> appeared to produce two summer generations in all three alkaline lakes, but in the more freshwater lakes there was evidence of only one generation per year.

When temporal distributions of instars are compared (figure 8) the last (third) summer generation in Barnes Lake for <u>C</u>. <u>expleta</u> was seen later than that for <u>C</u>. <u>bifida</u> (its second), although second generations of both were approximately contemporaneous, as they were in Lake Lye. In Round-up Lake juveniles of <u>C</u>. <u>expleta</u> persisted longer in the fall than those of <u>C</u>. <u>bifida</u> . Jansson and Scudder (1974) found a time-lag of about one week in the generations and demonstrated that the start of breeding was also slightly staggered, but they considered that the breeding patterns of the species were

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Figure 8. Temporal distribution of stages of C. bifida and C. expleta in six study lakes on Becher's Prairie, sampled at 4 day intervals in 1972. (i-v= first to fifth instars; a=adults).

1= Barnes, 2= Lye, 3= Round-up, 4= Greer, 5= Rock, 6= East Lakes.
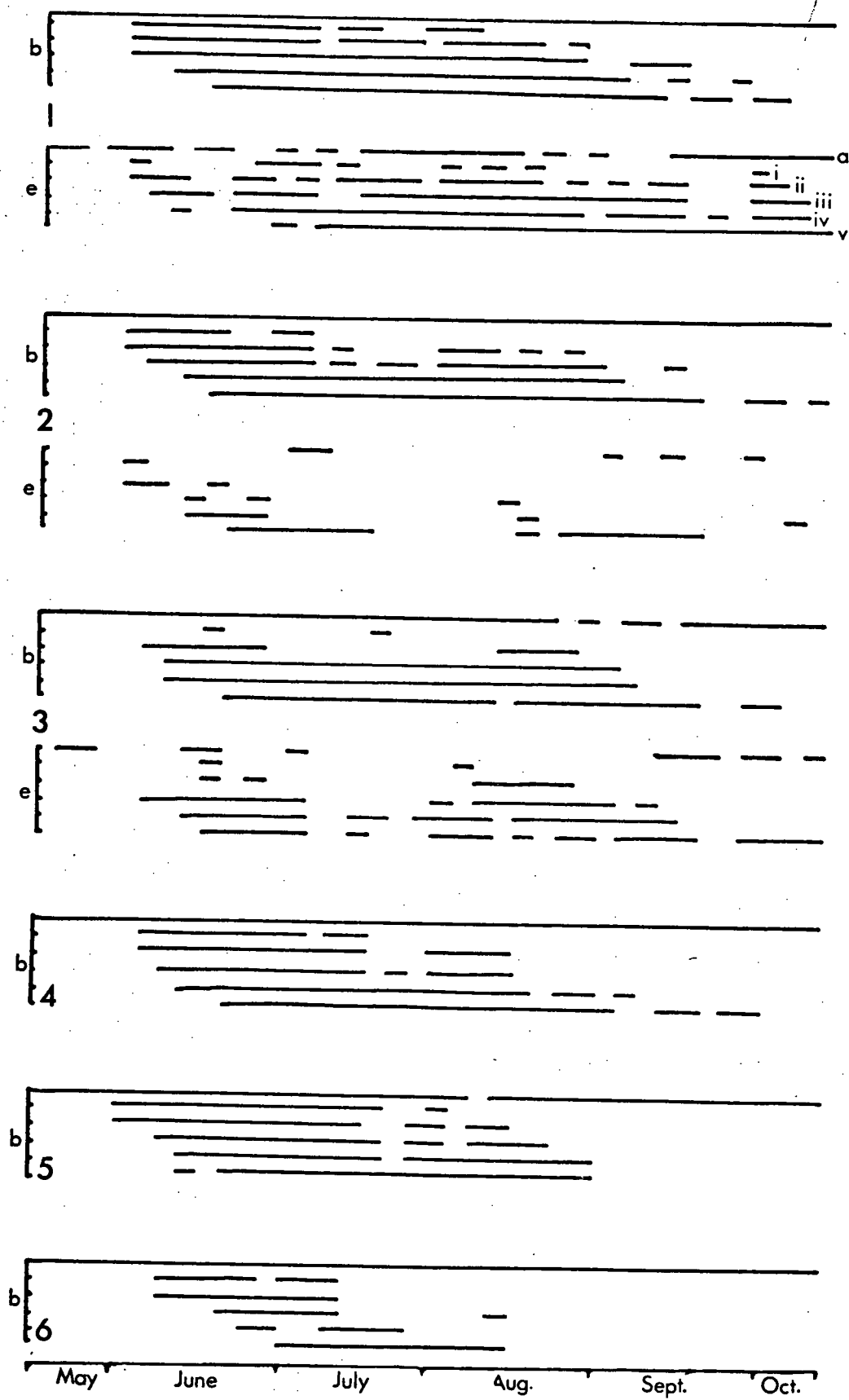
essentially contemporaneous. In the present study young instars of corixids were not detected in sweep-net samples before the end of May in the three high-alkaline lakes, and there is no marked indication of generation lag in sympatry, lending substance to Jansson and Scudder's (1974) conclusion.

Breeding populations of _Cymatia_ _americana_ Hussey, _Hesperocorixa_ _laevigata_ (Uhler), _Sigara_ sp. and _Callicorixa_ _audeni_ Hungerford also occurred in the freshwater lakes and their temporal distribution of instars is contrasted with data for _C_. _bifida_ (Figure 9). In each lake and species, there is one clear, temporally restricted generation in each year. _H_. _laevigata_ was found in all six Becher's Prairie lakes, but bred only in the three most freshwater. A similar pattern was found in _C_. _americana_ , but this species was never observed in Round-up Lake, and for _Sigara_ species - probably _S_. _decoratella_ (Hungerford) - which was not seen in either Barnes or Round-up Lakes. _C_. _audeni_ was locally abundant in the adult, and bred in East and Rock Lakes but not apparently elsewhere; it has not been recorded from Barnes Lake.

_C_. _americana_ , _H_. _laevigata_ and _C_. _audeni_ species seemed approximately contemporaneous with _C_. _bifida_ in the appearance of their summer generation. By contrast, _Sigara_ sp., which is very similar in size and appearance to _Cenocorixa_, unexpectedly showed an early summer generation in East Lake, the third instars being present by late May (figure 9) although the main groups of larval instars were contemporaneous with the rest.

Monthly means of corixid counts for all species and stages

Figure 9. Temporal distribution of stages of corixid species sympatric with C. bifida in the three freshwater lakes on Becher's Prairie, sampled at 4 day intervals in 1972.

b= C. bifida , c= C. audeni , cy= C. americana , h= H. laevigata and s= Sigara sp.

GREER

ROCK

EAST

May   June   July   Aug.   Sept.   Oct.
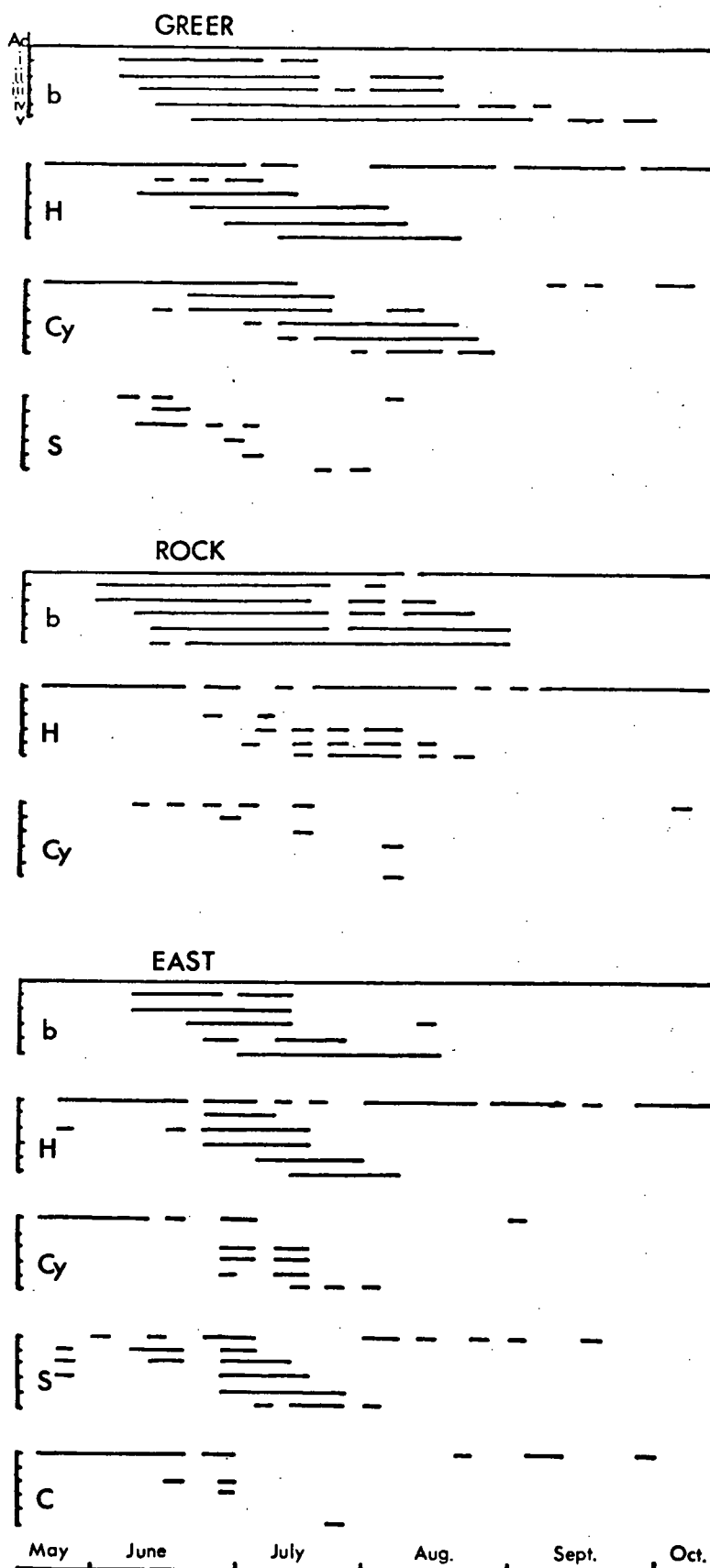
(figure 10) indicate that the mean number of corixids per ten sweeps is highest in Barnes Lake , the most alkaline, and lowest in East and Round-up Lakes. The highest numbers recorded were 5648 per ten sweeps in Rock Lake, chiefly recently eclosed first instars. Greatest numbers of corixids were present from June to August in each lake, reflecting the presence of many juveniles; September and October numbers were generally low (means under 200 per ten sweeps) in all lakes.

The proportion of adults of each sex at different seasons was examined for each lake and species, since the sexes could not be assumed to behave and feed identically. In Corixidae males emerge typically somewhat before females (Pajunen and Jansson, 1969a) which tended to skew the ratios towards males for the earlier part of each generation. Rearing and holding evidence also indicated a rather higher male mortality but no quantitative results were available.

Table XI summarises details of sex ratios for C. bifida . Overall, males were fewest in spring but slightly more abundant than females in midsummer and probably more so in fall. This suggests a relatively high male mortality in winter, a feature reported to be fairly frequent in Corixidae (Jaczewski, 1936; Larsen, 1938). A similar pattern was seen for C. expleta . The overwintering adults of C. americana , C. audeni and H. laevigata were predominantly female, but summer generation adults were almost equal in the first two species. In H. laevigata the early-emerging summer adults were chiefly males; as more females emerged the sex ratios returned closer to

Figure 10. Numbers of corixids per ten standard sweeps in each Becher's Prairie lake studied in 1972, expressed as monthly means.
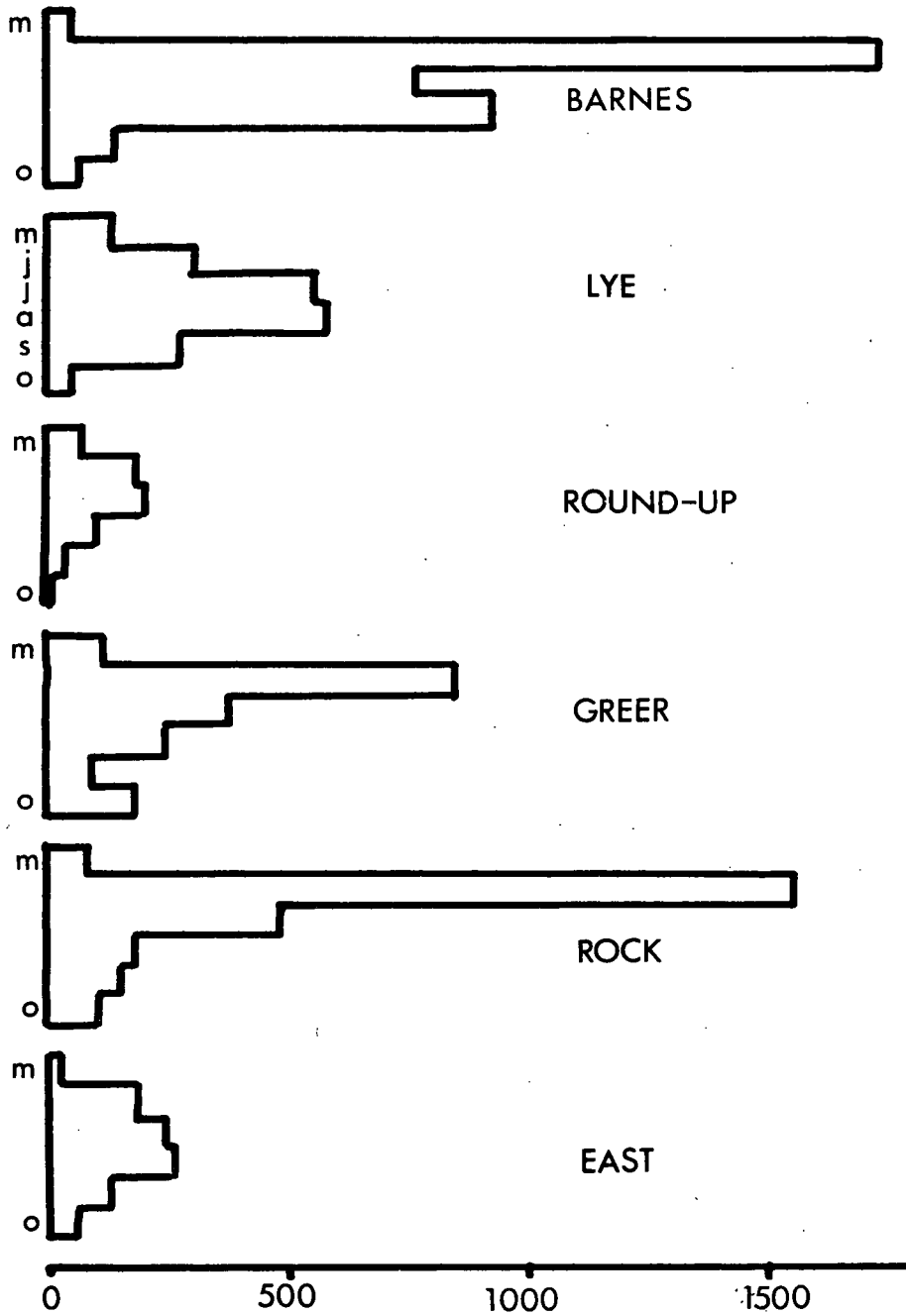
Table XI. Summary of sex ratios of <u>C</u>. <u>bifida</u> in samples, expressed as percentage of males, and total corixids examined (n).

	BARNES	ROUND.	LYE	GREER	ROCK	EAST	ALL:
SPRING (18 May-18 June)	52.8	43.4	45.5	46.5	42.1	53.2	46.4
n =	1112	632	1489	2143	1785	498	7659
SUMMER (18 June-28 Sep)	57.6	59.0	53.7	56.2	58.9	41.0	52.4
n =	1134	95	1374	610	846	1473	5521
FALL (October)	40.7	69.6	52.1	59.7	62.3	58.8	58.2
n =	59	23	71	414	138	97	802
ALL SEASONS	46.1	49.5	54.8	50.3	48.3	44.8	47.4
n =	750	2933	2301	3157	2769	2068	13982

equal in fall.

Habitat Surveys

Possible habitat preferences were investigated for the two species of Cenocorixa in the Becher's Prairie lakes, in a check for potential factors such as spatial segregation, that could lessen interspecific competition.

Scudder (1966) reported that in the field C. expleta preferred to oviposit on rocks, but C. bifida on decaying leaf-sheaths of flooded grass, while in captivity C. bifida oviposited on the plastic screening placed in jars for clinging to, and C. expleta primarily on the sides and floor of the jar itself. Jansson (1971) suggests that there may be analogous differences in habitat preference between the two species in the field, C. bifida preferring inshore, reedy areas and C. expleta the deeper waters with rocks and sandy bottoms, but he did not adduce any evidence to support this.

My studies on corixid oviposition did not entirely support Scudder's observations. Most C. bifida in captivity oviposited on both screen and container bottom, especially the latter, whereas C. expleta oviposited on the bottom alone in most cases, occasionally also placing a few eggs on the screen as well. Selection of oviposition site was thus not clear-cut between the species in captivity.

Habitat preferences in the present study were investigated from two standpoints; at midlake stations adult and juvenile corixids were collected whenever seen swimming near the surface, and inshore, surveys of different habitats were made on several different occasions in the three alkaline lakes.

Midlake sightings of corixids were commonest in spring and fall, when flight and dispersal may be most pronounced. Although adults were seen in most lakes studied, observations were considerably fewer in the three more freshwater lakes and here, midlake records were all for C. bifida .

Inshore and midlake collections in the three more alkaline lakes are contrasted in table XII. Midlake records of juvenile instars indicate that dispersing adults were not the only forms contributing to midwater lake populations, a point further corroborated by the absence of any records for C. expleta from the more freshwater lakes, even in midwaters. In alkaline lakes, the proportion of C. expleta was higher in midlake samples than inshore, suggesting that this species might prefer offshore waters or midwater situations to inshore benthic shallows. This was further investigated in inshore surveys.

Detailed investigations of contrasting habitats were made around the shores of Barnes Lake in June and September, 1972, and in July and August, 1973; in Round-up Lake in August, 1973 and in Lake Lye in mid-October, 1973, just before freeze-up. In each lake sites were selected with contrasting facies, such as gravelly, muddy and reedy.

Table XII. Midlake and inshore records of corixid occurrence in three lakes on Becher's Prairie (Data for matched dates only).

	BARNES	LYE	ROUND-UP	totals
MIDLAKE				
<u>C</u>. <u>expleta</u>				
adults	2	2	16	24
juveniles	2		2	
<u>C</u>. <u>bifida</u>				
adults	3	15	16	38
juveniles	4			
percent <u>C</u>. <u>expleta</u>	36.4	11.8	52.9	38.7
INSHORE				
<u>C</u>. <u>expleta</u>				
adults	12		3	44
juveniles	21		8	
<u>C</u>. <u>bifida</u>				
adults	54	479	246	1710
juveniles	477		2	
percent <u>C</u>. <u>expleta</u>	3.2	0.0	4.4	2.5

In June, 1972, habitats studied were all inshore, and included flooded <u>Juncus</u> and grass, muddy areas and shores near flooded trees. July (1973) samples were collected in similar regions, but inshore and offshore samples were collected at each site. August (1973) samples again came from inshore and offshore areas but only three of the original four stations were sampled. In September (1972) the four major stations were again sampled inshore and offshore.

The results for Barnes Lake are summarised in figure 11, where tentative isopercentile lines were fitted to sampling data, taking into consideration depth and habitat distribution patterns. Although relative abundance of <u>C</u>. <u>expleta</u> was many times greater in 1973 than in 1972, distribution patterns were not dissimilar. There were consistently higher proportions of <u>C</u>. <u>expleta</u> offshore than inshore, but as total numbers were also lower offshore than inshore (due perhaps partly to lowered sampling efficiency) this species may in fact be absolutely more numerous inshore than offshore, despite being relatively less abundant .

In Round-up Lake in August 1973 samples taken inshore and offshore at one place again indicated that <u>C</u>. <u>expleta</u> made up a higher proportion of offshore populations than inshore (61% versus 91%) but in Lake Lye just before freeze-up no <u>C</u>. <u>expleta</u> were among the 13 corixids taken there offshore. Since the overall proportion of <u>C</u>. <u>expleta</u> in combined samples was only 1.6%, these results are inconclusive. On the plain bottom habitat in Lake Lye <u>C</u>. <u>expleta</u> made up 9.5% of all corixids

Figure 11. Maps of isopercentile lines drawn for the percentage of <u>C</u>. <u>expleta</u> in samples taken at different habitats in Barnes Lake at four dates.

A= 24 June 1972. B= 12 September 1972. C= 17 July 1973. D= 25 August 1973.
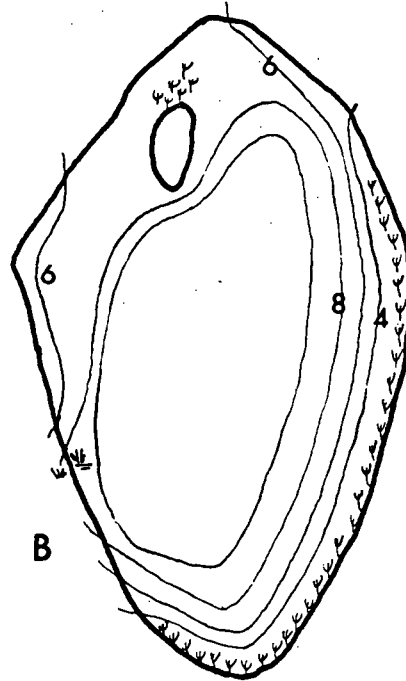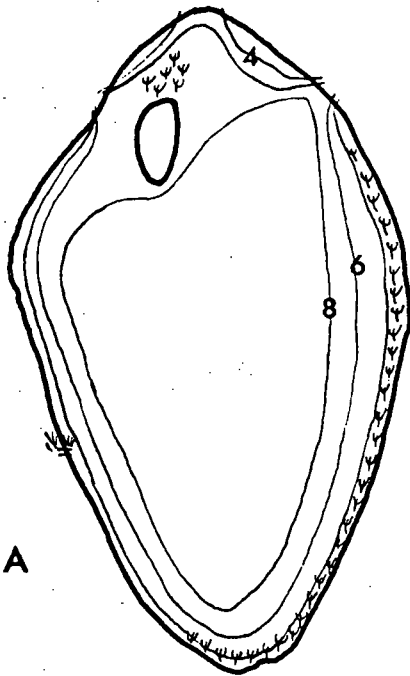
Scirpus

dead trees

A

B

C

D
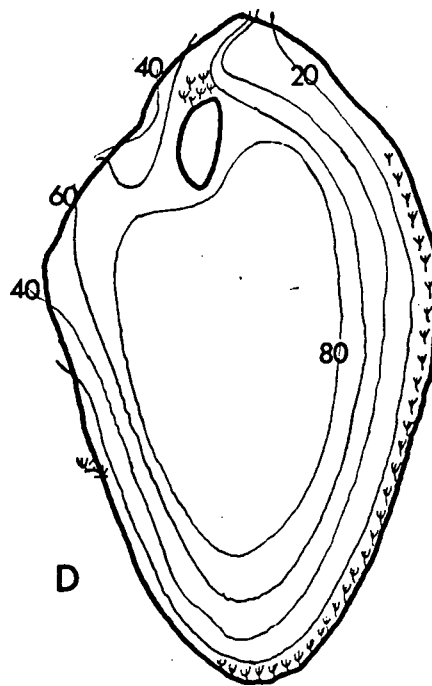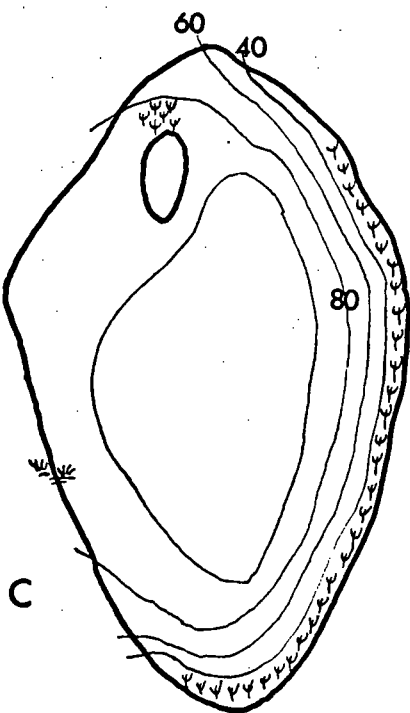
present, but was absent from shallow muddy areas or gravelly regions with _Juncus_ or logs.

In the Barnes Lake sequence _C. expleta_ was initially relatively more abundant over sheltered soft mud, but at the steeper sloping station among flooded trees the percentage dropped off rapidly during the summer, both inshore and offshore. Offshore highest numbers were obtained at the regular sampling site where the mud was relatively firm and logs and rocks were absent. Percentages were most variable over very soft mud or among flooded trees.

In contrast to the general preference of _C. expleta_ for a plain substrate and rather deeper water in the Becher's Prairie lakes is the situation at Lake LB 2, where this species was often found on the fringes of the shallow aquatic plant masses as well as on the silty bottom areas. Thus habitat preferences may be quite complex and conclusions drawn for one place may be untenable elsewhere.

Due to the slight generation lag between the species, habitat preferences of instars were not considered individually, but for Barnes Lake were grouped into instars one to three, instars four and five, and adults, for each season (figure 12). Comparisons indicated that the first preference of habitat for _C. bifida_ adults was plain mud only in June, and was mud with debris of various kinds at other times. In _C. expleta_ adults were commonest over offshore mud in July. Fourth and fifth instars of both species were usually found inshore, with those of _C. expleta_ being concentrated inshore on mud in July. The

Figure 12. Distribution of <u>Cenocorixa</u> species and instars in different habitats of Barnes Lake, at three times of year.

Bi= <u>C</u>. <u>bifida</u> , ex= <u>C</u>. <u>expleta</u> .
A= June, b= July, c=September.

Upper blank section of each diagram represents percentages of first to third instars; shaded area, fourth and fifth instars; lower blank area, adults.

1= mud and <u>Juncus</u>, 2= mud and twigs, 3=mud, 4=mud and logs, 5= <u>Scirpus</u>, 6= mud and rocks, 7= offshore mud, 8= offshore mud and rocks.

BI

1 2 3   4 3 6 7 8   4 1 5 2 3 7

A   B   C

EX
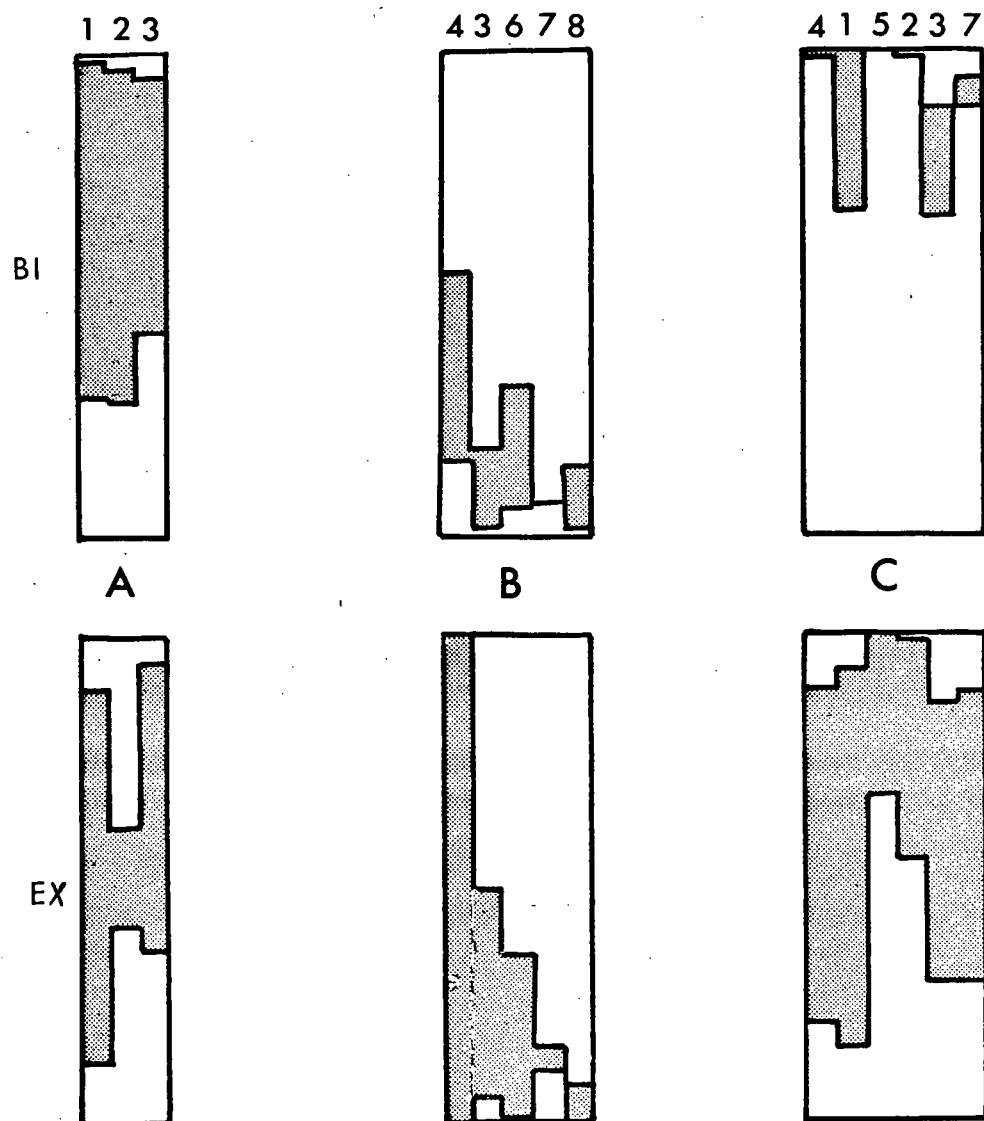
first three instars were predominantly found on inshore mud in June and September, being found offshore generally in July. Thus the inshore-offshore segregation of different instars, as shown by their percentage occurrence in each habitat, was most marked in mid-season, and at this time the distribution of instars of each species was also most dissimilar. By contrast, distribution of instars of both species followed a rather similar pattern in the September samples.

Although there emerges no seasonally consistent pattern of dominance of either species in any one facies, the smaller bodies of data from Round-up and Lye Lakes follow the pattern described for Barnes Lake. Little difference was seen between the species in facies or habitat preference in fall, except for effects related to the slight generation lag.

For all dates and lakes for each habitat (figure 13) the percentage of adult C. bifida among Scirpus , inshore mud, rocks and logs is higher than that for C. expleta , although each species had a similar order of preference for habitats. In the smallest instars C. bifida was more predominant over offshore mud than was C. expleta , but the larger juveniles of the latter preferred Scirpus, inshore mud, rocks, logs and offshore mud more than those of the other species. Thus, since fifth instar C. expleta are larger than the same instar of C. bifida , as a generalisation in both species, the largest individuals preferred the most diverse habitats.

Observations suggested that in C. bifida males tended to be grouped around obstacles such as logs, rocks inshore and reed

Figure   13.   Percentages   of   C. bifida   and   C. expleta
occurring in different habitats in the higher salinity Becher's
Prairie lakes in 1972 and 1973.

Ad= adults, bi= C. bifida , ex= C. expleta .

1= scirpus, 2= mud and logs inshore, 3= mud and twigs offshore,

4= mud and Juncus, 5= inshore mud, 6= offshore mud, 7= inshore

rocks, 8= offshore rocks and twigs.
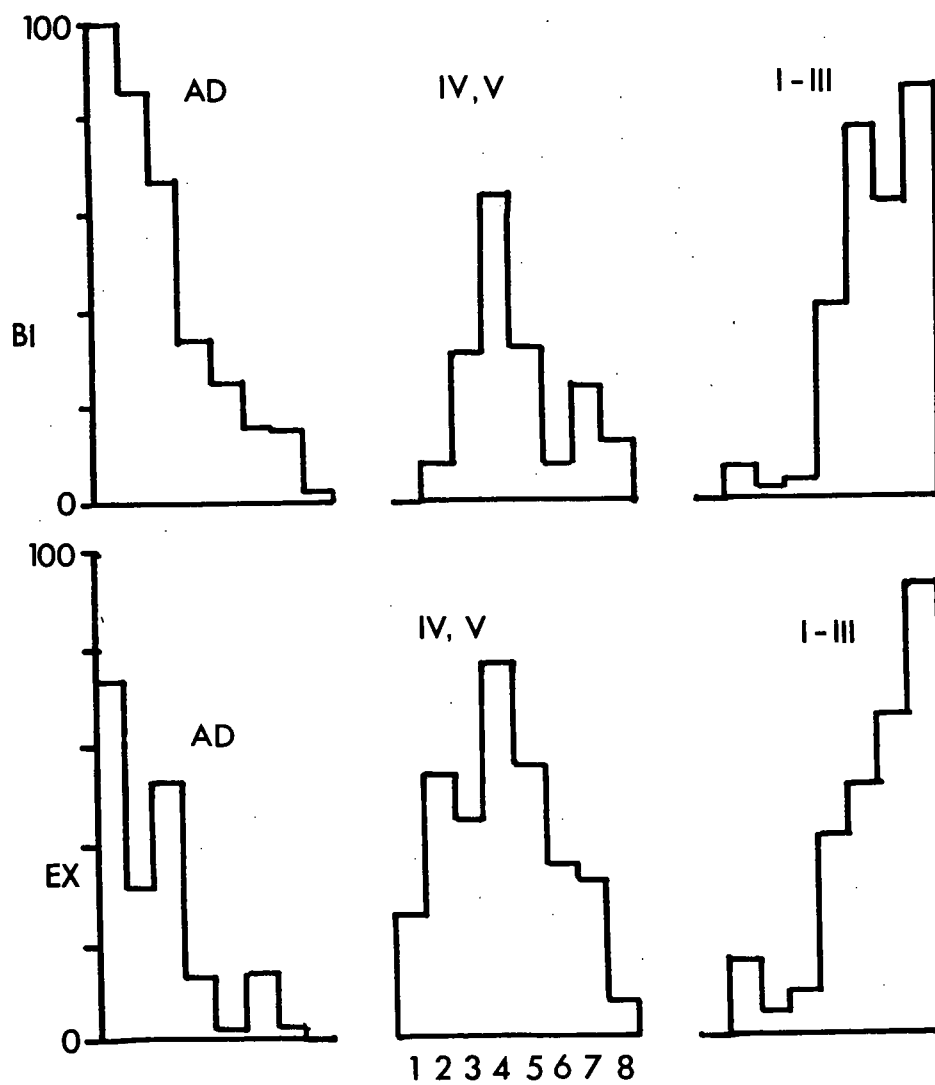
beds, whereas females were found most often in more open areas, not clustered in groups. Table XIII shows habitat distributions of corixids in mid-September, 1972, at Barnes Lake, arranged in order of increasing heterogeneity of habitat. It indicates that an increasing proportion of males was found in increasingly diverse habitats.

In summary, although habitat preference varies between sexes, instars, lakes and seasons, all data summed agree with midlake observations in indicating that, in sympatric situations, C. expleta shows some preference for deeper waters (over 40 cm) and for plain mud or silt bottoms (figure 14).

DISCUSSION

Corixids are known to have wide salinity tolerances (Rawson and Moore, 1944), although there is often marked variation between species groups (i.e. Sailer, 1948; Brooks and Kelton, 1967; Savage, 1971; Knowles and Williams, 1973). Scudder et al. (1972) reported differences in physiological tolerances of the two Cenocorixa species and linked them to their distribution in high saline waters, but suggested that since both have typically freshwater ionic and osmotic balances, C. expleta must be excluded from breeding in lakes with a conductivity of less than 5000 umhos cm⁻¹ through ecological interactions rather than physiological limitations. Jansson (1971) found that C. expleta

Table XIII. Sex ratios of adult _Cenocorixa_ in different habitats of Barnes Lake in September, 1972.

HABITAT	n (totals)	percent males
Plain mud	64	50.0
Mud with twigs	220	53.5
Mud and log	296	57.4
Mud and _Scirpus_	486	65.0

Figure 14. Overall percentages of C. bifida and C. expleta in samples from different habitats.

Bi= C. bifida , ex= C. expleta , G= gravel, Ju= Juncus, L= logs, M= mud, Sc= Scirpus, T= twigs.

Ju   T   L   L;T   M   M   G   Sc

0

EX

50

BI

0
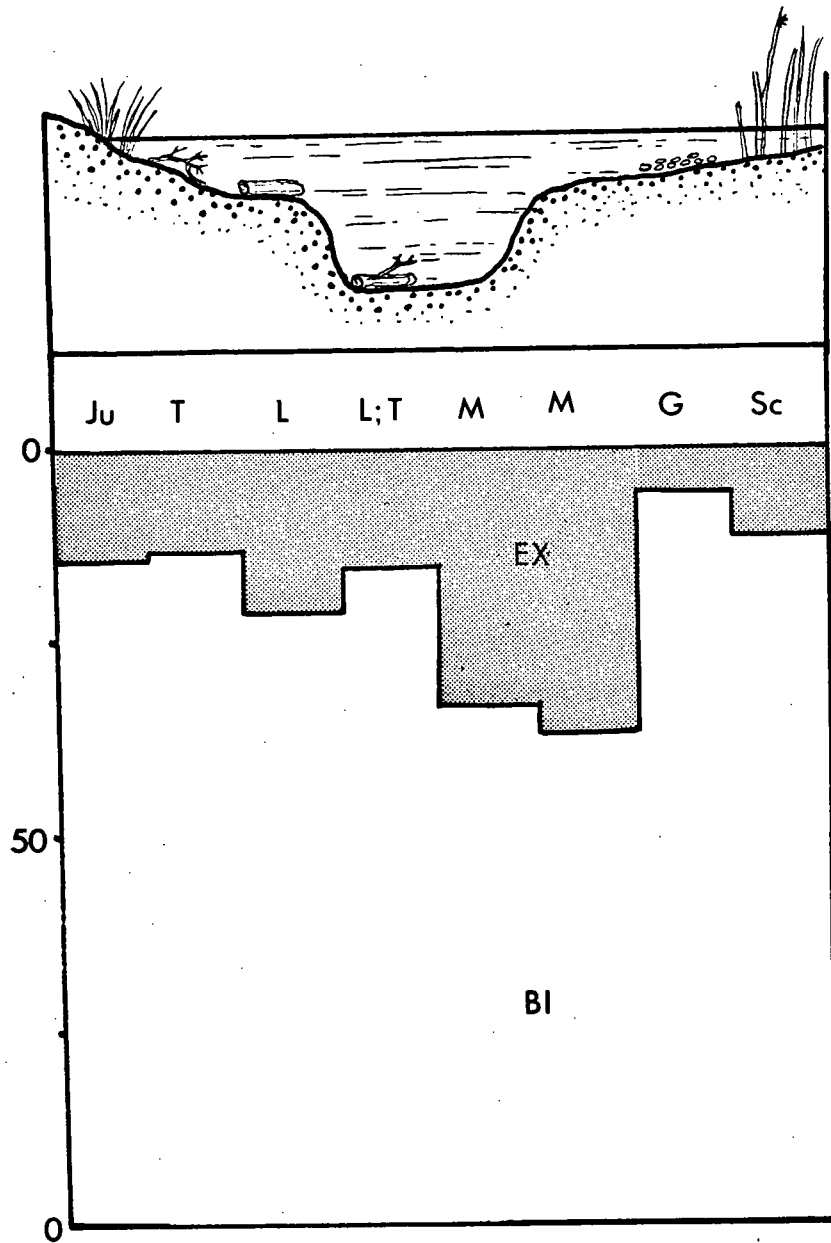
did not breed in field or laboratory at lower conductivities. However, I have reared $\underline{C}$. $\underline{expleta}$ eggs laid in Rock Lake water of conductivity about 1100 μmhos cm^{-1} to the second instar in the laboratory.

In the Canadian prairies corixids are abundant over a wide salinity range, but Brooks and Kelton (1967) found highest corixid densities in a lake of about 28,000 μmhos cm^{-1} conductivity, higher than anything investigated in the present study. Although mean abundances were highest in Barnes Lake, other parameters of abundance did not appear to follow any definite pattern with alkalinity, and in particular there were marked differences in corixid abundance between the rather similar lake pairs, Round-up and Lye, and Greer and Rock Lakes. The few corixids in Round-up Lake compared with their abundance in Lake Lye was also reflected in numbers of plankters and benthic organisms (Chapter II), and table VIII indicates that in the alkaline lakes corixids formed a greater proportion of the benthic faunal biomass than in the more freshwater lakes.

DeBach (1966) suggests that reduced numbers of two species in sympatry compared to their abundance in allopatry can be an indication of competition. However, numbers of $\underline{C}$. $\underline{bifida}$ and $\underline{C}$. $\underline{expleta}$ were greatly variable in allopatry and sympatry. Thus, one can deduce no evidence here for competitive interactions.

Of the corixids listed for the Becher's Prairie lakes (Scudder, 1969a) only $\underline{Dasycorixa\ rawsoni}$ was not recognised from the 1972-1973 samples; other species were confirmed in their

occurrence and some casual distributional ranges extended. Scudder (1969a) emphasised that the distribution pattern is not static, but changes with seasonal and longer-term differences in weather and climate.

Almost all species were recorded as casual visitors to each lake, except for C. expleta which was not seen in the three most freshwater lakes. In Lake LB 2 C. bifida appeared in the fall and has initiated breeding there the following spring in some years (Scudder, 1969a). Corixids are thus opportunistic in their distribution, the spring and fall dispersal pattern helping to ensure their widest possible survival (Johnson, 1966, Pajunen and Jansson, 1969 b; Pajunen, 1970a,b). Thereafter their breeding success must be regulated by other factors. Since they do not feed at low temperatures, their winter distribution represents neither specific conductance sensitivity nor food preference to any degree.

The present studies confirm previously established breeding patterns for Cenocorixa species (Scudder, 1969; Jansson and Scudder, 1974), indicating that in this respect as well as in physico-chemical data 1972 was a typical year. C. expleta seems to breed approximately contemporaneously with C. bifida , but may produce a third generation in the most alkaline lakes. This would give the former an advantage in years following a mild or prolonged fall, especially if there is some feeding or habitat segregation between the instars. C. expleta would then enter the following season with a greater number of adults than after a sudden fall cold spell or early winter, which would be likely to

kill off many juveniles before they could moult to the adult overwintering stage. Since the second generation of both species is approximately contemporaneous, adults of both this and the third generation may overwinter. However, since both species of _Cenocorixa_ were essentially contemporary in sympatry, there is no evidence for competitive interaction from phenology data.

Martin (1970) suggests that larger species usually develop slower, but start earlier, in sympatry. In terms of competitive strategy this does not seem to afford any selective advantage and it was not seen for either of the larger species _H. laevigata_ or _C. americana_ in the three more freshwater lakes in the present study. However, the early appearance of the summer generation in _Sigara_ sp., a species very similar in size and appearance to _C. bifida_ , may be a survival mechanism allowing coexistence with the latter, which is numerically dominant, by permitting the nymphs to develop earlier to a size where they do not compete with those of the dominant species.

Development of corixids seems most favoured in the more saline lakes on Becher's Prairie; _C. expleta_ having two or three, and _C. bifida_ two generations per year in sympatry, whereas in the three more freshwater lakes _C. bifida_ and the other corixid species produced only one generation per year. _C. expleta_ also produced two to three generations in the high salinity Lake LB 2 (Scudder and Jansson, 1974). Numbers of generations per year are related by Jansson (1971) primarily to food availability, rather than to photoperiod or temperature initiating ovarian arrest, and the previous chapter has

demonstrated that although biomass of benthic organisms was greatest in the freshwater lakes, there appeared to be ample food in all lakes, and a steadiest supply of plankton, particularly of diaptomids, in the more saline lakes studied.

C. bifida only breeds successfully in Lake LB 2 in spring, and its later exclusion there seems correlated with increasing salinity as the dilute surface waters gradually become mixed in. However, exclusion of C. expleta from the more freshwater lakes may not be a result of osmotic tolerance limits (Scudder et al., 1972) but rather because of ecological requirements. Thus, Jansson (1971) suggested the possibility of partial geographic or ecological isolation as a potential isolating mechanism for Cenocorixa sibling species, noting that where the species coexisted in the Chilcotin area of B.C., C. bifida was chiefly found at pond edges in reed beds but C. expleta chiefly in deeper waters, rather like the distribution patterns of the coexisting species of Sigara described by Macan (1938). Martin (1970) also noted that coexisting corixid species tended to feed "in different areas" of a pond.

Brooks and Kelton (1967) give some ecological information for corixid genera in Canada, and suggest that Cenocorixa spp., particularly C. expleta , are usually found in large, sandy lakes, often saline, and lacking conspicuous vegetation. In contrast, C. americana , H. laevigata and some C. audeni and Sigara species prefer areas with some vegetation. However, in the freshwater Becher's Prairie lakes C. bifida was the most abundant despite extensive weed development, and in Lake LB 2

C. expleta was often found on shallow weed-masses, perhaps a convenient resting place from which to dart out on their prey.

According to Brooks and Kelton (1967) the majority of corixids are most abundant in conditions apparently not suited to heteropteran predators such as Notonecta species. Fernando (1959) suggested that food and suitable habitats seem to be the density-dependent factors ultimately limiting corixid populations, but added that predators may be responsible for much of the mortality in crowded or less than optimal conditions. Predators on corixids in the Becher's Prairie lakes may include waterfowl, which Bird (1961) noted feeding on corixids in similar water-bodies, especially in the fall when duck numbers are greatest and aquatic plants have become less dense. Since predators of corixids will eliminate first the most obvious colour mis-matches , according to Popham (1941), these might help to keep the paler C. expleta out of the more freshwater lakes. Predation as a possible exclusion factor, especially for the younger instars, was not further investigated here. However, swimming patterns may differ slightly between the two Cenocorixa species, or feeding habits may make some instars and species more conspicuous to intending predators than others.

Distribution results will obviously be influenced by the development success of each generation, which is linked to site of oviposition. Drowned trees might initially have offered suitable oviposition substrates for both species in Barnes Lake (possibly vertically segregated to correspond to their observed preferences), but the areas might subsequently have proved less

favourable for C. expleta and numbers of this species then dwindled either through predation (ambush predators being well provided with concealment) or through some other factor such as the high organic content of the soft mud. Diaptomus sicilis swarms were particularly abundant among the trunks of flooded trees, suggesting that food abundance itself was not necessarily a direct factor (see chapter IV).

The presence or absence of aquatic macrophytes and filamentous algae is related to conductivity level in the six Becher's Prairie lakes studied (Chapter II). This suggested that corixid distribution might be affected by plant development as much as by salinity per se, and habitat checks helped to corroborate this. C. expleta was least frequent in sympatric lakes amongst Scirpus, Juncus and branches, showing preference for a plain silty bottom with little heterogeneity (as summarised in figure 14). C. expleta also seems to be more frequent in midlake than C. bifida , perhaps representing greater mobility in open waters. Similarly, Corixa germari is also recorded as preferring offshore waters (Crisp, 1962 b); this species, like C. expleta , markedly prefers to oviposit on stones, although it will also deposit its eggs on vegetation.

C. bifida on the other hand was most abundant among rocks, logs and emergent rushes and reeds. However, the segregation between the species is by no means absolute, and since corixids are most numerous inshore, perhaps the greater mass of the population is sympatric here. Nonetheless, some spatial segregation of the species or instars would help to lessen

competition for space and food; the latter factor will be considered in more detail in chapters IV and V.

CHAPTER IV. FEEDING EXPERIMENTS

INTRODUCTION

There is little agreement about the diet of Corixidae. Some authors (i.e. Martin, 1970; Jansson and Scudder, 1972) see them as predators or carnivores, others (i.e. Parsons, 1966) consider them to be essentially herbivorous and microphagic. For a few species there is some observational evidence to support both contentions, although Istock (1973) states that "...good information on food habits does not exist for even a single species, and would be difficult to obtain...". Gut studies in particular are cited as unsatisfactory by several authors, i.e. Crisp (1962 b), since food ingested is largely liquid and amorphous.

It seems likely that corixids will accept a wide variety of foods, both animal and plant, dead and alive. Thus, while Puchkova (1969) finds that Corixidae have a mixed type of feeding, with a predominance of phytophagy, Zwart (1965) reported the survival of Corixidae was longest in captivity when fed on an animal diet.

Some information on food habits of a species may be obtained by feeding individuals under controlled conditions and observing their reactions to the foods offered. Such findings are not directly applicable to the species in nature because of the artificial experimental situation and the fact that through

ignorance their preferred items of diet may not be offered. Numerous studies, e.g. Hsiao and Frenkel (1968) and Jamieson (1973) have shown that if a preferred food item is not chosen by the experimenters, one can expect the behaviour of the experimental animal to be atypical. Further, some authors, e.g. Latheef and Harcourt (1972) have indicated that a herbivorous animal may respond best in tests, in terms of the amount eaten and acceptability, to foods which may be poorly suitable for growth and reproduction. Jamieson (1973) questions whether such a difference in response is important in carnivores, suggesting that qualitatively one animal prey may be similar to another in terms of usefulness. Whether this is in fact true or not, observations of the behaviour of animals in feeding experiments give an idea of their capabilities of handling particular items of prey, give data against which gut contents can be compared, and provide one view of the differences between the species with respect to their ability to use available food items, alone or in combination. They thus provide one indication of the dietary parameters of the fundamental niche.

PRELIMINARY EXPERIMENTS

Initial experiments were run to test feeding potential of C. bifida and C. expleta in various experimental situations, and to determine their survival time without food. Observations by Scudder (unpublished) indicate a maximum survival time at 25 C without food of around ten days. However, below 5 C, as when overwintering, feeding ceases and corixids can be stored for

considerable periods with little mortality.

Preliminary observations were made in January, 1972 using Cenocorixa blaisdelli and diaptomids from a small pond on the U.B.C. Campus. Corixids were isolated in filtered, dechlorinated water and offered various entomostracans. At 5 C nc feeding was observed but survival was good. However, at laboratory temperatures (24 C) mortality of corixids and prey crganisms was high. Fungal growth was prevalent on dead organisms, and in extended experiments it was difficult to determine if prey death was due to corixid predation or some other factcr. Diaptomids usually appeared to have been bitten through the carapace at the junction of cephalothorax and abdominal segments, and their contents partly sucked cut; this was easily determined with bright red copepods but was not so easy with other entomostracans. Cyclopoid copepods, which leave similar evidence of feeding, (Walters, personal communication), were not mixed with diaptomids in this experiment. It was apparent that direct evidence of feeding would be required and this wculd have to be observed taking place.

Further preliminary experiments, at Becher's Prairie in May, 1972, investigated the feasibility of different experimental methods and factors such as size of test enclosures and viability of organisms. In general, corixids adequately survived crowding at densities of ten per 100 ml water. Survival was improved with regular cleaning of dishes and changing of the test water. However, owing to the difficulty cf cbserving feeding and the relatively high mortality rates, long-term

experiments were not judged to be suitable.

Adult C. bifida were shown to eat dead and live plankters, chironomid larvae, amphipods and zygopterans. After periphyton was added to one dish, corixid faeces seen subsequently were greenish, indicating that some plant matter might also have been used as food. No hydracarinids, coleopteran larvae or ephemeropteran nymphs were eaten.

Using the information gained in the preliminary tests, a series of controlled, short-term feeding experiments was initiated in the summer of 1972 and continued into 1974. The methods devised and used and the results obtained are described below.

MATERIALS AND METHODS

Corixids were collected by the use of a dip-net, throughout the summer season in 1972, 1973 and 1974 at all experimental lakes, thus encompassing the range of habitats encountered. They were placed in insulated 2 litre flasks partly filled with water from the same lake, for transport to the laboratory; they survived for up to two days with little mortality under these conditions. Corixids not immediately used for experiments were held in circular plastic 5 litre troughs at 5 C, at which temperature they do not feed (Jansson and Scudder, 1972).

Prey organisms were collected similarly or by plankton tows. In some cases these were supplemented with organisms from

the U.B.C. Campus ponds and from lakes Marion and Eunice in the U.B.C. Research Forest, Haney. Prey used (Table XIV), included groups of organisms that occurred frequently in the studied lakes and so might be suspected to form part of the diet.

Before testing, corixids were starved so that they might be uniformly receptive to food: preliminary experiments indicated that 24 h at laboratory temperature was most appropriate. Too prolonged starvation of an animal may make it less selective of food, but such an effect was not noted in this test. The feeding response of C. bifida starved for two days was compared with that of one-day starved animals from the same location and collection date. Feeding was found to be more prolonged and intense in the two-day starved corixids (a mean of 1.5 feeding bouts observed over ten 20-second periods of observation, n=46) than in the one-day starved forms (mean 0.8 bouts, n=109). However, attack and 'intention movements' were somewhat more frequent in those starved for the one day period than for two days (means 2.7 and 2.3 attacks per individual respectively). Jamieson (1973) found that a similar food deprivation interval of 24 h for larvae and 48 h for adult Gerridae (Heteroptera) was sufficient to attain maximum ingestion in feeding tests. In the present tests, the 24 h period was used throughout.

Corixids were individually isolated in dishes containing 125 ml of filtered lake water from their home lake, and a 2 cm square of plastic to cling to. Three slightly different container types were used interchangeably for experiments. Preliminary tests using C. bifida fifth instar nymphs collected

Table XIV. Details of prey organism groups used in feeding experiments, with numbers of tests using each.

PREY	SIZE,SPECIES DETAILS	TESTS
Daphniids	_Daphnia pulex, D. schodleri, D. magna, D. similis_ (carapace length 2.0-2.7, mean 2.4 mm)	205
Dead daphniids	same forms	161
Diaptomids	_Diaptomus sicilis, D. nevadensis_ (length 0.8 - 3.0 mm)	177
Dead diaptomids	Same forms	132
Mixed small plankton: _D. sicilis, Ceriodaphnia_ sp.		175
Dead mixed plankters: Same forms		68
Fairy shrimp	_Branchinecta_ sp. from LE 2	55
Dead fairy shrimp	Same forms	21
Amphipods	_Gammarus lacustris, Hyalella azteca._ (smaller than corixid tested)	161
Dead amphipods	Same forms	132
Hydracarina	Water-mites, red or black	16
Chironomid larvae	Mixed forms, 4.0-6.5 mm, mean 5.5 mm long	229
Dead chironomids	Same forms	117
Chaoborid larvae	_Chaoborus americanus_	44
Dead chaoborids	Same forms	4
Zygopteran nymphs	_Enallagma_ species (smaller than corixid tested)	85
Dead zygopterans	Same forms	113
Ephemeropterans	_Callibaetis_ species nymphs, (smaller than corixid tested)	102
Dead ephemeropt.	Same forms	56
Beetle larvae	Smaller than corixid tested	24
Juvenile corixids	_C. bifida_ first and second instars	4
Macrophytes	_Potamogeton, Ruppia, Ceratophyllum, Myriophyllum_ species	20
Algae	Cladophora-type and blue-greens	20

at one sampling place and date, plus two 'active' prey types (daphniids and diaptomids) and one 'passive' prey type (chironomid larvae) showed no marked differences in corixid response between the different container types (Table XV).

At the start of each single prey type feeding experiment, and in those using a mixture of planktonic organisms, a potential food was added to dishes containing starved corixids. Prey offered were almost always smaller than the corixid being tested. Each animal was then examined ten times at approximately ten minute intervals, for a period of 20 seconds at each examination. During this examination period, corixid reactions were scored as

    0 : no reaction directed to food.

    1 : flutter movement made by stationary
    corixid, involving rapid palar motion, usually
    in reaction to abrupt movement of prey close
    by. Corixids typically showed fast brushing of
    the abdomen with the hind limbs.

    2 : swimming corixids lunged at prey, singly
    or repeatedly, but did not succeed in
    capturing it. This movement was different from
    exploratory or flight-oriented movements.

    3 : swimming or stationary corixid made a
    sudden swimming lunge at a prey, capturing it
    momentarily.

    4 : corixid captured and fed on prey organism
    for more than five seconds of the observation
    period. Feeding corixids made the same fast

Table XV. Feeding response data for C. tifida in different types of test containers, when fed similar prey types. (For test conditions see text description).

CONTAINER TYPE	ATTACKS (MEAN PER DISH, 10 STUDY PERIODS)	FEEDING (MEAN PER DISH, 10 STUDY PERIODS)	REPLICATES
350 ML PLASTIC DISH	1.9	1.6	38
250 ML PLASTIC BEAKER	2.2	1.6	25
250 ML GLASS BEAKER	2.0	0.8	5

movements of the hind limbs described in reaction level 1.

When more than one reaction type occurred in one observation period, only the reaction of greater intensity was noted. At the conclusion of each experiment the water temperature was measured and for each corixid species and instar and, if adult, sex and whether teneral or old, was recorded, along with the colour of the food in the gut. This was distinguished on a zero to five point scale (0=empty, 1=yellow, 2=tan, 3=red, 4=brown, 5=olive-greenish). In larval instars and sometimes in the young adults food material could be seen directly through the body wall, but in most adults, cr where little food was ingested, dissection was necessary to observe the gut contents.

Reactions to the prey were not quantified on an intensity gradient, as there seemed to be no clear relationships between the number of intention movements (reactions 1 or 2) in the experimental situation, and feeding success. Further, under the system of notation used, multiple reactions to a prey in one time period were recorded as single only. In the collation of results, specimens which showed no reactions to prey were included, although there may have been reasons for their lack of response, such as damage during transfer to the experimental dish, or imminent moulting.

Moults occurred on 33 occasions (1.6%) in the 2127 feeding trials with single prey types. Feeding experiments indicated that feeding can apparently take place up to five minutes before

ecdysis and as soon as 15 minutes after the moult is complete. Many factors, such as the softness and ease of capture of the prey offered, may affect this time-period, and in most cases feeding ceased some time before the moult (mean of observations 70 minutes) and the last intention movement ceased at a mean of 40 minutes before ecdysis. After the moult, feeding started again after a mean lag of 40 minutes. Data collected within 70 minutes before and 40 minutes after moults were therefore eliminated from the analysis.

Oviposition caused apparently little or no disruption of feeding. In several instances eggs were laid in dishes in which the experimental corixid was apparently feeding for much of the observation period.

In the analysis of results, each experiment was assessed, and if corixid behaviour was listed as levels 3 or 4 (capture or feeding respectively) in any of the ten observation periods, the experiment was considered positive evidence for feeding on that prey, while intention movements (level 1 or 2) were considered as negative, along with no reactions (level 0). This broad treatment of the results minimised any possible bias which might have been introduced through the use of different experimental containers. Data were summed for each species. For further analysis, data were subdivided by sex and instar, and placed in categories relating to the environmental diversity, as follows :

      lake group 1 : C. expleta from Lake LB 2

      lake group 2 : C. expleta and C. bifida from

      Barnes and Round-up Lakes and Lake Lye

lake group 3 : C. bifida from Greer, Rock and

East lakes.

Season 1 : May and June

season 2 : July and August

season 3 : September and October.

For the prey choice feeding experiments, except those using mixed plankters, initial procedures were identical to those described above, but each dish was observed continuously and all corixid reactions recorded under the same headings as before. Once feeding had occurred, the experiment was terminated in each case, thus avoiding problems of removal and replacement of prey to prevent distortion of prey ratios in a continuing experiment. Numbers of mixed small plankters used were so great that this effect was not judged important.

Computer programmes to scan the data, describe each experiment as positive or negative evidence of feeding on each prey type, and tabulate the results by corixid species and instar, prey, season and lake group, were kindly written by Ms. Dolores Lauriente. Other statistical calculations were done using the U.B.C. Computing Centre programmes CHI 2 and SAS 1.

RESULTS

Structure and Behaviour

During the experiments some insight was gained into feeding behaviour and its relation to structure of mouthparts and alimentary canal. Most evidence pointed to carnivory, rather than to a phytophagous habit.

In test situations corixids alternated bouts of rapid, restless swimming with periods spent picking over the bottom of the test dish or the plastic screen with palae and mouthparts, or clinging motionless to the screening. Preliminary observations suggested that corixids swam more frequently when live prey were present than with dead prey. However, an analysis of the frequency of bursts of undirected swimming activity showed no significant differences between the two situations, indicating that the proportion of distraction or 'startle' swimming is not likely to be great in each case. The picture is rather different when 'intention movements', specifically directed towards the food item, are considered.

Data matched for date or lake of origin were analysed to see if major differences existed in feeding intensity between live and dead prey. In all corixids intention movements of intensity levels 1 to 3 were more frequent with live prey in experiments than in those with dead (Table XVI). Thus, although some activity may have been the result of distraction or startling by the potential food organism rather than of interest in it, a living prey aroused more directed corixid activity than

Table XVI. Intensity of corixid activity when offered dead and live preys. (Data for <u>C</u>. <u>bifida</u> ; activity registered as intention movements recorded in ten observations in each feeding experiment. Intensity levels described in text; levels 1 and 2 = directed interest, level 3 = prey clutched, level 4 = feeding from prey).

level :	LIVE PREY				DEAD PREY			
	4	3	2+1	n=	4	3	2+1	n=

PREY TYPE :

AMPHIPODS	7	15	101	59	53	1	4	43

Mean 2.09 activities/   Mean 1.35 activities/
individual,   individual,
 1.71 for levels 2+1   0.09 for levels 2+1

CHIRONOMIDS	120	5	75	120	126	2	25	50

Mean 1.67 activities/   mean 3.06 activities/
individual,   individual,
 o.63 for levels 2+1   0.50 for levels 2+1

PLANKTERS	24	2	198	45	79	7	204	98

Mean 4.98 activities/   mean 2.96 activities/
individual,   individual,
 4.40 for levels 2+1   2.08 for levels 2+1

a dead one.

Prey motion may attract initial attention through mechanisms such as vision or pressure detection. Dead prey, on the other hand, may be seen or discovered by chance during a restless activity bout, or through following a chemical gradient to the food-source. When the freshly killed prey were halved, the body juices entering the water of the test dish produced faster corixid orientation to the cut prey than to an intact prey organism.

Live prey organisms were not always detected by the corixids (as determined by feeding lunges cr intention movements) unless they were within striking distance, generally about 1.5 mm away. Similarly, corixids often seized a previously ignored prey when it was moved close to them and held in a fine forceps. However, corixids were excited at a greater distance to spasmodically swimming organisms, on occasions lunging across the width of the test dish (6 to 7 cm) to take a prey. Late instars and adults could also sometimes be enticed to attack the point of a needle if this was moved through the water to a position 1 to 2 mm from their rostrum in a jerky fashion.

Thus, motion of the prey seems to be an important trigger initiating feeding behavicur, although since corixids became excited by prey motion below and behind them, vision cannot be the only means of detection. The behaviour of both juveniles and adults thus strongly suggests carnivory and limited predation. Feeding on plants was more difficult to corroborate, and when it seemed to occur it was rarely accompanied by rapid hind-limb

beating as seen in corixids feeding on animal prey.

To capture a prey organism, the corixid pounced rapidly and scooped it in the palae, a motion bringing it tightly adpressed to the mouth region. Then, if prey orientation was correct, feeding could commence. Many adult corixids presented with a prey held in a forceps gripped it with their palae so firmly that the corixid could be lifted out of the water for some seconds by raising the forceps.

Adult and juvenile C. bifida were observed to catch and hold diaptomids to the rostrum for up to 10 seconds before dropping them, still alive. This may have been due to incorrect orientation; diaptomids were usually sucked through the dorsal carapace, leaving a characteristic crushed or broken area. They were also sucked occasionally through the antenna. Similarly, a Daphnia caught and held by the carapace spine for 35 seconds escaped unharmed, only to be recaptured and reoriented for successful feeding, which was usually observed to occur through the ventral area between the valves. Sutton (1951) noted that corixids frequently pierced daphniid eyes for feeding; perhaps the black colour provided visual orientation for close manipulation and selection of feeding site.

Thus, once a corixid has captured a prey organism, subduing of the prey apparently depends on factors such as integument toughness as much as on the reported venomous secretions of the maxillary glands (Sokol'skaya and Zhiteneva, 1973). Once subdued, body juices were rapidly sucked out and a starved corixid could capture and feed on several large chironomid

larvae or one to two fairy shrimps in one hour, these being quickly reduced to empty skins or shrivelled bodies. However, when prey were abundant, a corixid would often abandon a partially-eaten organism for another living one, a feeding habit also noted by Walton (1943b).

Recording of feeding was relatively easy for some prey; soft-bodied forms shrank or lost their colour as juices were sucked out. In other cases the prey had to be examined after being released by the corixid for signs of damage or death and loss of turgor. Also feeding corixids usually beat their hind limbs regularly, at about one half to two beats per second, considerably faster than the balancing or grooming movements seen when at rest. Occasionally when the corixid was facing the prey or its own reflection the same rapid limb beating occurred, followed sometimes by a swimming lunge. Sutton (1951) described a similar brushing of the abdomen with the hind legs when a corixid became aware of a prey; it then darted to face the prey and hovered with stationary rowing motions producing water currents which might help immobilise the prey, before pouncing upon it.

Wherever possible corixids were presented with test food organisms smaller than themselves, although with certain forms, as plants, or when testing the smallest corixid instars, this was not feasible. The problem of prey size and attack success discussed by Jamieson (1973) for gerrids, was not further investigated here, and it was mitigated in analysis of results by including levels 3 and 4 in evidence of feeding. Thus prey

size was not such a critical factor as it might have been if only successful capture leading to feeding (level 4 alone) were considered as positive evidence of feeding on that prey. Adult corixids would attack a fairy shrimp more than twice their length; attacks here were not usually successful unless directed to the tail. Corixids rarely showed any response to larger ephemeropteran or zygopteran nymphs, but when the same prey organisms were provided dead the corixids approached without hesitation and fed from them. Again, many corixids seemed to actively avoid amphipods even when these were clearly smaller than themselves; this might be due to the regular and rapid swimming of the amphipods around the container, since dead amphipods were usually seized immediately. Thus, preference for different prey may have been as much mechanical, concerned with the logistics of catching and grasping, as based on biotic conditions, a conclusion Jamieson (1973) also came to with gerrids.

In the experiments visual assessments were made of gut colour after each test on a six point scale, as described above. Results of these records are summarised in Table XVII. For all 645 corixids tabulated the gut colours most frequently seen were colourless, red or brown. However, considering only those corixids recorded as feeding on the prey offered, the proportions of colourless guts not unexpectedly declined, and red guts became dominant. This is chiefly a result of feeding on diaptomids and mixed plankters; chironomid larvae, even bright red in colour, contributed mostly to the brown colour category.

Table XVII. Corixid gut colour after offering known preys in feeding experiments. Dominant colour underlined for each prey type.

GUT COLOUR :	0 empty	1 yellow	2 tan	3 red	4 brown	5 olive	n =
PREYS :	PERCENT SHOWING EACH GUT COLOUR AFTER TESTING						
Daphniids	14.3	21.4	8.3	13.1	<u>42.9</u>	0.0	84
Diaptomids	5.8	8.8	9.5	<u>72.3</u>	3.7	0.0	137
Mixed plankton	5.8	4.6	4.6	<u>71.3</u>	13.8	0.0	87
Amphipods	14.3	14.3	0.0	0.0	<u>71.4</u>	0.0	7
Chironomids	12.0	20.0	10.0	4.0	<u>54.0</u>	0.0	50
TOTALS	32	45	29	174	86	0	365
PERCENT EATING FOOD OFFERED	8.7	12.3	7.9	47.5	23.5	0.0	

Colours were observed through the body wall, which would account for some dulling of the hue. The range from brown to yellow through tan seemed similar both for chironomids and the relatively colourless daphniids, probably reflecting the amounts of either consumed.

Single Prey Experiments

Twenty-three potential prey items, of which two were plant and nine were freshly-killed animals, were tested in 2127 single-prey experiments with approximately equal numbers of C. bifida and C. expleta (Table XVIII).

The numbers of each species and instar tested depended upon their availability and proportions in samples collected, as corixid juveniles could not be identified to species without microscopic examination which might cause stress or damage. Thus no tests were run for dead Branchinecta or juvenile corixids with C. bifida , nor for aquatic macrophytes or algae with C. expleta . However, fairy shrimps were uncommon and vernal in those lakes which contained both Cenocorixa species and plant life was inconspicuous in the higher salinity lakes inhabited by C. expleta (see Chapter II).

Results indicate that both C. bifida and C. expleta fed very similarly overall, taking most items offered (Table XIX). Refusals of food items were generally attributable to their large size or activity relative to the corixid instars tested. Neither species took hydracarinids and, among items tested for

| | Cenocorixa bifida | | | | | | | | Cenocorixa expleta | | | | | | | |
| FOOD ITEMS | INSTARS | | | | | ADULTS | | | INSTARS | | | | | ADULTS | | |
	1	2	3	4	5	f	m	TOTAL	1	2	3	4	5	f	m	TOTAL
Daphnia		13	16	28	36	17	21	131		10	10	15	10	19	10	74
Dead Daphnia	1	11	15	10	13	15	14	87		12	10	12	10	18	12	74
Diaptomus		4	15	32	29	13	14	107		11	14	10	11	13	11	70
Dead Diaptomus	1	11	13	17	11	14	8	75	2	10	13	8	10	12	12	67
Mixed plankton		9	10	16	18	4	16	73		6	24	24	14	19	15	102
Dead mixed plankton			1	1	1	14	8	25			9	14	14	3	3	43
Branchinecta			1	2	3	4	3	13			3	4	10	12	13	42
Dead Branchinecta								-			3	8	10			21
Amphipods		2	7	14	24	16	12	83		2	11	10	10	26	18	77
Dead amphipods			1	1	28	11	9	58		6	10	18	11	20	9	74
Hydracarina					3	1		4						5	7	12
Chironomids			11	20	13	25	21	108		21	17	29	28	15	11	121
Dead chironomids		2	7		6	17	8	40	1		10	10	12	21	22	76
Chaoborids						15	5	20						18	6	24
Dead chaoborids						1	1	2						1	1	2
Zygopterans		3	10	11	11	4	2	47			10	2	3	14	7	36
Dead zygopterans			1		1	13	16	41			11	14	13	24	10	72
Ephemeropterans			1		7	10	12	30		2	16	22	15	10	7	72
Dead ephemeropterans			1					9		6	17	10	14			47
Coleopterans				4	5	1	2	12				1		5	6	12
Juvenile corixids								-						2	2	4
Algae					1	9	10	20								-
Macrophytes						7	13	20								-
								1043								1084

Table XVIII. Numbers of replicate feeding experiments with each foodstuff for each species and instar of Cenocorixa (totals columns includes unsexed adults).

Table XIX. Summary of results of feeding experiments testing 2127 corixids with 23 different single food items (x = food item offered and accepted; - = item offered but not accepted)

	C. BIFIDA						C. EXPLETA				
INSTARS	1	2	3	4	5	ads	1	2	3	4	5	ads
FOOD ITEM												
Daphniids		x	x	x	x			x	x	x	x	x
Dead daphniids	-	x	x	x	x			x	x	x	x	x
Diaptomids	x	x	x	x	x			x	x	x	x	x
Dead diapt.	-	x	x	x	x		-	x	x	x	x	x
Mixed plankton	x	x	x	x	x			x	x	x	x	x
Dead mixed pl.		x	x		x			x	x	x	x	
Fairy sprimp		-	-	x	x			x	x	x	x	
Dead fairy sh.								x	x	x		
Amphipods	x	x	x	x	x		-	x	x	x	x	
Dead amphi.		x	-	x	x		x	x	x	x	x	
Hydracarina				-	-							-
Chironcmids		x	x	x	x		x	x	x	x	x	
Dead chiro.	x	x		x	x		-	x	x	x	x	
Chaoborids					x							x
Dead chaob.					-							x
Zygopterans	-	x	x	x	x			x	x		-	x
Dead zygopt.		-		x	x			x	x	x	x	
Ephemeropt.		-		-	x			-	-	x	x	x
Dead ephem.		x			-		x	x	x	x		
Beetle larvae			x	x	x					x		x
Juv. corixids												-
Macrophytes					x							
Algae				-	-							

one species of <u>Cenocorixa</u> only, <u>C</u>. <u>bifida</u> did not take dead chaoborid larvae or algae while <u>C</u>. <u>expleta</u> similarly did not take juvenile corixids. The feeding pattern revealed for both species is definitely carnivorous and largely predatory. Thus in overview, their fundamental niches did not differ markedly, suggesting that in feeding pattern at least, the species might be considered ecologically homologous.

However, Chapter II has shown that the proportions of food items available for testing varied from lake to lake and from month to month in each lake. It is therefore possible that diet, as indicated by the results of feeding experiments, will differ with season of collection and lake of corixid origin. As juvenile corixid instars also differed markedly in size, motility and appearance and to some extent also in habitat preferences from each other and from adults (Chapter III), it is likely that their feeding habits will also show differences. To investigate such possible differences, which could have marked effects in the field on potential competition for food, the data were first examined in terms of adults alone and then subdivided by lake and season.

(i) Feeding patterns of adult _Cenocorixa_ collected in different lakes :

Corixids collected from different lakes might be expected to have a certain dietary preference related to conditions in their lake of origin at the time of collection. The longer they are kept before testing, the more this possible preference pattern could be expected to diminish in the artificial conditions of low-temperature storage and crowding.

To test whether such a preference is evident in the feeding experiment results and therefore might bias the analyses if ignored, feeding data for adults from different lakes were compared (Table XX). Most data were too few for statistical analysis, but there seem to be no consistent trends towards different feeding intensities on the foodstuffs listed, among corixids from different lakes. In _C. bifida_ collected in the higher salinity lakes on Becher's Prairie there was a non-significant trend towards more feeding on dead amphipods than in those collected in the lower salinity lakes, where the foodstuff occurs naturally (Chapter II), but this is likely to be a result of the few data available.

Thus no statistically significant differences between corixids collected from different lakes were observed, and therefore different lake data were pooled in further analysis of the feeding patterns.

Table XX. Comparison of results of feeding experiments using adult _Cenocorixa_ collected from different lake groups. (Lake group 1: LB 2. Lake group 2: Barnes, Round-up and Lye. Lake group 3: Greer, Rock and East Lakes).
Data expressed as percentage of corixids successfully feeding; and probability between lakes, from chi squares.

		_C._ _expleta_				_C._ _bifida_		
	LAKE	percent feeding	n=	p=	LAKE	percent feeding	n=	p=
FOOD ITEM:								
Daphniids					2:	53.8	13	0.8235
					3:	69.2	13	
Dead daphn.	1:	38.1	21	0.7351				
	2:	100.0	2					
Dead amphipods					2:	33.3	6	0.3594
					3:	0.0	10	
Ephemeropterans					2:	8.3	12	0.5444
					3:	10.0	10	
Chironomids	1:	79.2	24	0.7997	2:	61.1	36	0.9266
	2:	50.0	2		3:	50.0	10	

(ii) Feeding patterns of adult Cenocorixa collected at different seasons :

Since fewest corixids were collected in spring, feeding patterns of adult corixids collected in July and August were compared with those for corixids collected later in the year (seasons 2 and 3 respectively; Table XXI). Although there were no significant differences between the different seasons with any foodstuff, C. bifida collected in summer fed more on daphniids and amphipods than did those collected in fall. A similar trend was seen for C. expleta feeding on zygopteran nymphs, but when this species of corixid was offered dead amphipods, feeding tended to be greater in those collected in fall than among those from the summer.

The results thus indicate that corixids collected at different times of year showed no statistically significant differences in feeding intensity on any of the prey offered. The few non-significant trends seen did not follow a consistent pattern seasonally for all foods. This may again be a result of the variable, but often prolonged storage cf corixids before testing, and may mask real differences in feeding preference or intensity such as seem to be present in field-collected animals, from serological analysis of their gut contents (Chapter V).

Table XXI. Comparison of feeding experiment results for adult
Cenocorixa collected at different seasons. (Season 1: May-June.
Season 2: July-August. Season 3: September-October).
Data expressed as percentage of corixids successfully feeding, and
probability between seasons, from chi squares.

FOOD ITEM:	C. bifida percent feeding season	n=	p=	C. expleta percent feeding season	n=	p=
Daphniids	2: 70.0 3: 0.0	23 4	0.2829	2: 69.2 3: 50.0	13 14	0.8724
Dead daphniids				2: 25.0 3: 46.2	8 13	0.8240
Diaptomids	2: 58.3 3: 0.0	12 1	0.7428	2: 30.0 3: 46.2	10 13	0.8685
Dead diapt.				2: 53.8 3: 66.7 t8	13 3	0.7495
Dead mx. pl.	2: 20.0 3: 35.3	5 17	0.9101			
Amphipods	2: 50.0 3: 0.0	4 18	0.0841	2: 18.5 3: 7.7	27 13	0.7510
Dead amphip.				2: 0.0 3: 56.5	4 23	0.3715
Ephemeropt.	2: 0.0 3: 14.3	8 14	0.7833			
Zygopterans	2: 50.0 3: 0.0	2 8	0.5993	2: 25.0 3: 0.0	12 9	0.4312
Dead zygopt.				2: 100.0 3: 58.3	2 24	0.9285
Chironomids	2: 51.6 3: 73.3	31 15	0.6588	2: 75.0 3: 80.0	16 10	0.8232
Dead chiron.				2: 46.2 3: 77.3	13 22	0.5615

(iii) Feeding patterns of _Cenocorixa_ males and females :

Among the adults studied, female _C. bifida_ ate more items offered than did males, but the same was not obvious in _C. expleta_ (Table XXII). Females of both species ate rather more dead foods than males (p=0.3908 for _C. bifida_ , p=0.2531 for _C. expleta_) but results were less conclusive for live foods where female _C. bifida_ ate more than males (p=0.4770) but the reverse was seen for _C. expleta_ (p=0.6622). Male _C. bifida_ ate more diaptomids than did females (p=0.3480) whereas the females ate more chironomid larvae than did males (p=0.1879). All these trends are statistically non-significant at the five per cent level, and results of adults are not therefore considered separately by sex in the general analysis of the results.

(iv) Feeding patterns of teneral and old adults of _Cenocorixa_ :

In feeding experiments a trend was seen towards more feeding in young teneral forms than in the older adults (Table XXIII). This was marked in _C. bifida_ , but the few data for _C. expleta_ were anomalous in that both forms fed at similar intensity levels. No trends appeared to be significant, and as most data were not distinguished to teneral or older adult, the results were summed for further analysis.

Table XXII. Differences in feeding pattern between the sexes of _Cenocorixa_ , from feeding experiments. Data expressed as percentage of positive feeding results per experiment.

FOOD ITEM :	C. bifida female (%)	n=	male (%)	n=	C. expleta female (%)	n=	male (%)	n=
Diaptomids	28.6	14	53.8	13	45.5	11	30.8	13
Dead diapt.	87.5	8	21.5	14	33.3	12	41.7	12
Daphniids	52.4	21	51.9	17	50.0	10	63.2	19
Dead daphn.	14.3	14	20.0	15	66.7	12	33.3	18
Mixed plankton	46.2	26	42.9	14	20.0	5	22.2	9
Dead mx. pl.	25.0	8	35.7	14	33.3	3	0.0	3
Amphipods	0.0	12	18.8	16	11.1	18	19.2	26
Dead amphip.	11.1	9	18.7	11	55.6	9	45.0	20
Fairy shrimp	33.3	3	25.0	4	8.3	12	41.7	12
Chironomids	71.4	21	48.0	25	81.8	11	73.3	15
Dead chiron.	37.5	8	17.6	17	68.2	22	66.7	21
Zygopterans	0.0	2	25.0	4	14.3	7	14.3	14
Dead zygopt.	31.3	16	30.8	13	70.0	10	50.0	24
Coleopterans	50.0	2	0.0	1	50.0	6	20.0	5
Chaoborids	20.0	5	13.3	15	33.3	6	22.2	18
Dead chaob.	0.0	1	0.0	1	0.0	1	100.0	1
Ephemeroptera	16.7	12	0.0	10	0.0	7	10.0	10
Juv. corixids					0.0	2	0.0	2
Hydracarina			0.0	1	0.0	7	0.0	5
Macrophytes	15.4	13	14.3	7				
Algae	0.0	10	0.0	9				
TOTALS	33.7	205	28.1	221	40.4	171	38.1	247
ALL PLANKTON	38.4	99	37.9	87	45.3	51	39.2	74
ALL DEAD FOOD	31.3	66	23.5	85	58.0	69	47.5	101
ALL LIVE FOOD	39.8	118	34.2	120	28.7	101	32.2	146

Table XXIII. Summary of data on feeding intensity cf tenerals versus older adult Cenocorixa.

SPECIES:	TENERALS percent feeding	n	OLD percent feeding	n
C. bifida	68.8	77	51.2	84
	chi square probability p=0.3106			
C. expleta	60.0	15	61.1	18
	chi square probability p=0.7889			

(v) General feeding pattern of Cenocorixa adults :

Twenty-one food items common or frequent in the lakes studied were tested with 454 adult C. bifida and 19 fccds with 439 adult C. expleta . Results expressed as percentage acceptance of each foodstuff are contrasted in Figure 15. This indicates, first, that C. expleta in general accepted more prey items in tests than did C. bifida , and also that the percentages of items eaten by the two species often differed markedly. Both species took chironomid larvae most frequently of all foods, but in general C. expleta preferred dead crganisms to living. Thus, when percentage feeding is ranked for each item of prey, mean rank of all dead organisms eaten by C. expleta was 6.6, compared with 11.4 for C. bifida which does not show the same bias.

The most marked differences between the species on individual foodstuffs entailed a greater feeding intensity of C. expleta than C. bifida upon dead chircnomid larvae (p=0.0639), dead daphniids (p=0.1346), dead amphipods (p=0.1480) and dead zygopteran nymphs (p= 0.3138). On the other hand, live mixed small plankters were rather more frequently taken by C. bifida than C. expleta (p=0.4450).

None of these trends are statistically significant, but they indicate a definite tendency of C. expleta tc prefer dead organisms more than does C. bifida , which seems to take dead and live items about equally, and to have a rather more planktonic food-base. The difference in feeding between the

Figure 15. Percentage acceptance of food items offered to adult C. bifida and C. expleta in 893 tests.

Results arranged in order of acceptance by adult C. bifida :

Data for C. expleta shaded.

	C. bifida		C. expleta
PREY		n	n
Chironomids		32	26
Daphniids		38	29
Dead diaptomids		22	24
Diaptomids		27	24
Coleopterans		3	11
Dead mixed plankton		22	6
Mixed plankton		20	34
Fairy shrimp		7	25
Dead chironomids		25	43
Dead zygopterans		39	34
Dead daphniids		37	30
Chaoborids		20	24
Macrophytes		20	-
Dead amphipods		28	29
Ephemeropterans		22	17
Amphipods		36	44
Zygopterans		12	21
Dead ephemeropterans		8	-
Dead chaoborids		2	2
Algae		19	-
Hydracarina		1	12
Juvenile corixids		-	4

species on dead chironomid larvae is particularly striking.

(vi) General feeding pattern of Cenocorixa juveniles :

In each species immature forms showed generally higher feeding levels, in terms of percentage acceptance of prey, than did adults. In C. bifida , more juveniles than adults took dead plankters, and in both species, other dead food items were also more eaten by juveniles than by adults. In C. expleta , the first six food items ranked by frequency of feeding for all juveniles combined were dead prey, as were eight out of the first ten in C. bifida juveniles.

Among juveniles of Cenocorixa species differences were not as marked as they were in adults. A fairly similar pattern of food acceptance was seen for members of the same instar group, irrespective of species. This is shown in Figure 16, where data are grouped for the first three instars and for instars four plus five.

In both small and large instars, C. bifida took relatively more daphniids, dead or alive, than did C. expleta . The smallest instars of C. bifida also took relatively more small mixed plankters than did those of C. expleta , although this position was reversed in the larger instars. C. expleta took more diaptomids than did C. bifida in small instars, but both species took about equal numbers in instars four and five. Numbers of replicate tests were too few for definite trends to

Figure 16. Percentage acceptance of food items offered to small and large instars of C. bifida and C. expleta . Results arranged in order of acceptance by adult C. bifida ; data for C. expleta shaded.

$I_1 - I_3$ $I_4 - I_5$

PREY	BI n	EX n	BI n	EX n
Chironomids	11	38	51	37
Daphniids	19	20	64	25
Dead diaptomids	25	23	28	18
Diaptomids	19	25	61	21
Coleopterans	-	-	9	1
Dead mixed plankt.	19	30	34	38
Mixed plankton	1	9	2	28
Fairy shrimp	1	3	5	14
Dead chironomids	9	11	6	22
Dead zygopterans	1	11	1	27
Dead daphniids	27	22	23	22
Dead amphipods	1	16	29	29
Ephemeropterans	1	18	7	37
Amphipods	9	13	38	20
Zygopterans	13	10	22	5
Dead ephemeropt.	1	23	-	24
Algae	-	-	1	-
Hydracarina	-	-	3	-
Dead fairy shrimp	-	3	-	18

0   100   0   100 %

be indicated for other prey. Juveniles of both species seemed to take less chironomid larvae than did adults, and more dead plankton.

Significant differences in feeding intensity on different prey were seen between different instar groups, but these followed no consistent pattern between species and for all foods. In the main, the youngest instars fed least on the items offered, adults occupied an intermediate position while fourth and fifth instars were the most active feeders. This is evidently related to the fact that the largest instars are also those most actively growing.

Table XIX indicates that first instar nymphs of both species did not feed on any prey offered, but only three foodstuffs were tested in only five replicate experiments overall. However, second and larger instars fed voraciously on anything they could tackle, notably the smaller mixed plankters and on dead food at first, taking more interest in live foods at larger stages. The species have been successfully reared through several generations on frozen brine shrimp (Jansson and Scudder, 1972) suggesting that first instar nymphs, if they feed at all, may be able to utilise dead animal food, unless they exist on protozoans or other microscopic life forms. Their scavenging habit in the youngest stage would follow from the increasing dependence on dead foods with decreasing size of instar seen already.

(vii) Summary of <u>Cenocorixa</u> feeding pattern :

Overall, <u>C</u>. <u>expleta</u> significantly preferred dead to live
foods (p=0.0000) although the same trend, seen in <u>C</u>. <u>bifida</u> ,
was not significant (p=0.3060). Thus, <u>C</u>. <u>bifida</u> ate a
significantly higher proportion of live foods than did
<u>C</u>. <u>expleta</u> (p=0.0023) but vice versa for dead foods (p=0.0003).
This difference has been shown above to be a result of feeding
differences in the adults and larger instars; <u>C</u>. <u>bifida</u> as
immatures prefers dead foods to live as strongly as did
<u>C</u>. <u>expleta</u> , but in later instars this preference becomes less
evident.

Significant differences were seen between the species
overall in their consumption of dead chironomid larvae
(p=0.0530), dead ephemeropteran nymphs (p=0.0073), dead
zygopterans (p=0.0073) and dead amphipods (p=0.0465), in all of
which <u>C</u>. <u>expleta</u> consumed significantly more than <u>C</u>. <u>bifida</u> .
However, with dead plankters there was no evident difference
between the species. The same similarity in diet of the two
species was seen for all live plankters and for ephemeropterans,
amphipods, beetle larvae and <u>Branchinecta</u>, but <u>C</u>. <u>expleta</u> took
more chaoborids than did <u>C</u>. <u>bifida</u> , although the predator and
prey in this case did not coexist in the Becher's Prairie lakes.
In summary, although both species ate the same foods,
fundamental niches were demonstrably not identical on closer
examination, and the species cannot therefore be considered true
ecological homologues.

Experiments with choice of prey

In preliminary experiments C. bifida adults accepted dead diaptomids, live daphniids, chironomid larvae, live diaptomids and live amphipods in that order of preference, when presented with a mixture of prey. Further experiments were therefore carried out to determine reactions to specific prey mixtures, and results are given in Tables XXIV and XXV.

Mixed small plankton, consisting largely of Diaptomus sicilis with some Ceriodaphnia species was collected from Barnes Lake in July and August, 1972. Five replicate subsamples from a plankton concentrate for mid-July, 1972, had a mean ratio of 94.2% Diaptomus to 5.8% Ceriodaphnia .

For the six dates when 59 C. bifida were tested, the ratio of prey eaten showed a marked reversal of proportions in the test samples, indicating a distinct preference for the slower-moving Ceriodaphnia. However, of 96 C. expleta tested on eight dates in the same months, the ratio of prey eaten was much closer to proportions in the lake at that time (Table XXIV). When dead plankters from the same source were offered as prey, patterns for each species did not change markedly, thus discounting ideas that differences in corixid agility, or in response to plankter motion, might produce the results.

When larger plankters were mixed with the smaller ones, there seemed to be distinct selection for the larger forms. Other tests using plankters were too few to be significant.

Table XXIV. Feeding success of C. bifida and C. expleta when offered natural mixed plankton, live and dead (Natural ratio of plankters 942 : 58 Diaptomids to Ceriodaphnia).

PREY	C. bifida			C. expleta		
	number eaten	times natural ratio	tests n =	number eaten	times natural ratio	tests n =
Live plankton						
Diaptomus	5	0.2		41	0.9	
			59			96
Ceriodaphnia	17	13.3		10	3.4	
Dead plankton						
Diaptomus	9	0.7		54	1.0	
			25			43
Ceriodaphnia	5	6.0		6	1.7	

Table XXV. Feeding success, expressed as percentage of strikes and of feeding in each test, with mixed preys.

LAKES	BARNES C. bifida			ROCK C. bifida			LE 2 C. expleta		
	feed (%)	strike (%)	N=	feed (%)	strike (%)	N=	feed (%)	strike (%)	N=
PREY :									
Daphniids	24.1	75.9		25.0	280.0		37.5	387.5	
			29			20			8
Chironomids	65.5	34.5		45.0	100.0		50.0	300.0	
Daphniids	55.0	80.0		41.7	150.0		71.4	185.7	
			20			12			7
Zygopterans	10.0	50.0		8.3	75.0		14.3	71.4	
Chironomids	83.3	94.4		65.0	125.0		42.9	85.7	
			18			20			14
Zygopterans	5.6	100.0		0.0	120.0		21.4	185.7	

In further tests in 1974, 67 C. bifida from Earnes Lake and 52 from Rock Lake on Becher's Prairie were presented with mixtures of a plankter (Daphnia), a benthic mud organism that sometimes enters the water column (chironomid) and a littoral organism (zygopteran). Results are given in Table XXV.

The reaction of C. bifida to the choice situation was so similar between the different lakes of origin that it lends weight to the conclusion, above, that there is no significant difference in corixid behaviour or prey preference attributable to lake of origin, under the test situation used. Overall, C. bifida first preferred chironomids, then daphniids, feeding on zygopteran larvae at a much lower level in choice situations. However, when only unsuccessful feeding attacks were tabulated (same Table) attacks were definitely greatest on daphniids, followed by almost equal numbers of attacks on the chironomid larvae and the zygopteran nymphs. Hence, although plankters may attract the most responses from a predatory corixid due to their almost continuous motion and small size, there seemed to be no definite preference for either chironomids or zygopterans of a definite size although the latter was less easily subdued or captured.

A further set of experiments with C. expleta from Lake LB 2 was run using the same prey organism combinations, and although fewer organisms were available for testing (Table XXV) results followed a similar pattern to that seen for C. bifida .

Foods accepted by other species

In preliminary tests, several H. laevigata adults were offered various foods, and were seen to accept a range of these similar to that demonstrated for C. bifida and C. exrleta . In particular, H. laevigata took dead chironomids, live and dead amphipods and zygopteran nymphs, but avoided hydracarina. In the main series of experiments a second instar nymph, inadvertently included for testing, fed on a dead chironomid and a fourth instar took a live zygopteran naiad.

Thus, although data for this species are scanty, the results indicate a similar feeding pattern for H. laevigata and Cenocorixa in terms of foods accepted in feeding tests. This topic is investigated further in the following Chapter, where guts of field-collected insects were examined by serological techniques.

DISCUSSION

The literature on corixid feeding extends back almost 200 years. However, since it has been summarised to some extent by Hungerford (1919) and more recently by Griffith (1945), only key references before the latter date will be mentioned here.

The earliest mention of corixid feeding habits is found in

De Geer (1788) who stated that they are carnivorous; this was generally accepted and corroborated with supporting evidence until the second decade of the present century. Thus, Westwood (1871) quoted a friend's report that _Corixa_ _ovivara_ in Indian streams fed on the spawn of _Barbus_ sp. Furneaux (1904) described corixids as "cannibals" and Buenc (1909) mentioned their "exceedingly hot tongue".

Similar deductions were also made from morphological studies, i.e. Dufour (1833), after describing the limbs, concluded that corixids were carnivores and Geise (1883) considered the barbed mandibular stylets to be useful for seizing simple animals. In the same vein, Kalgatz (1911) and others stated that the forelegs were well adapted for grasping small organisms and clutching them to the mouth while juices were being sucked out. Poisson (1923) cited toxic maxillary glands and the small pharangeal teeth as evidence of carnivory. However, some morphologists had doubts about the carnivorous suitability of the limbs; for instance, Bueno (1916) reversed his earlier opinion and suggested that _Rhamphocorixa_ may not in fact be carnivorous, since it was "not fitted with the means to seize living things ".

White in 1873 had carefully watched _Corixa_ scraping the surface of a rock on which were algae and rotifers, and then passing the palae rapidly and alternately to the mouth. However, until 1917 most authors considered corixids, like other aquatic hemipterans, to be carnivores. In that year Hungerford examined guts of one genus, finding disorganised plant matter and entire

algae, and concluded that the family as a whole represented "producers"; he thus ranked them with the Entomostraca in importance. He observed all instars of corixids stripping the chlorophyll from filamentous algae and, although he also saw them capture live animal prey, he stated that this did not represent the "usual feeding behaviour" (1917a,b, 1919). His morphological studies again stressed this; "corixids possess the most obvious adaptation of their limbs to definite vegetative feeding of any water bug...", the relatively large intake canal also allowing intake of some solids. However, he also recorded first instar C. americana as being cannibalistic (Hungerford, 1923).

About the same time Riley (1918) found diatoms and Oscillatoria in guts, and he assumed these organisms were collected from the surface of the ooze. However, he pointed out that even the highly predatory gerrids also feed occasionally on vegetable matter, particularly small fruits, suggesting that plant feeding may similarly not be dominant in corixids, but rather an incidental feature. Hungerford (1919), however, believed in a fundamentally microphytic diet for corixids.

Since that date, Hungerford's prestige has led to corixids being generally considered algal and detritus feeders, although a body of evidence for carnivory continued to accumulate. Many studies showed corixids to be sometimes important predators on mosquito larvae, in Australia (Hale, 1922), Haiti (Woolcott, 1927), Alaska (Jenkins, 1948) and Canada (Jenkins and Knight, 1950; James, 1966), mostly summarised in Sailer and Leink

(1954).

However, Griffith (1945) reinforced the microphytic diet idea with her studies of _Rhamphocorixa_ in Kansas which she reared to maturity on a _Typha_ (reed) infusion, although she pointed out that this contained not only algae but protozoans, rotifers, _Cyclops_, _Daphnia_, ostracods, snails, clams and chironomids. Stomach contents, although often unrecognisable, chiefly included finely comminuted algal remains. Hungerford (1948), describing this as the diet of the "average corixid", showed evidence of a corixid sucking _Spirogyra_ filaments and cited this as "conclusive proof of the herbivorous tastes of a water boatman", stating that that the abundance of this food is an explanation of the numerical abundance of corixids in many water bodies. He suggests, as does Walton (1943 a), that evolution of corixids represents a gradual alteration from predation to a microphytic diet , with the shortening of the stylets and rostrum, enlargement of the pharynx and mastigatory apparatus and adaptation of the pala from a raptorial to a sifting function.

Most recent reports of corixid feeding include an observation by Macan (1962) that _Glaenocorisa propinqua_ captured and fed upon zooplankters. Crisp (1962 b) found that adults of _Corixa germari_ fed in laboratory and field upon chironomid and lumbriculids, and nymphs ate small chironomid and dead first and second instars of their own species. Puchkova (1969) offered _Sigara striata_ a mixture of foods, and concluded that phytophagy was predominant in their diets, although various invertebrates

were also accepted. Planktonic crustaceans did not attract the bugs in the same way as did the tube-dwelling organisms such as _Tubifex_ and tendipedid chironomids. Peters and Ulbrich (1973) also indicated a predominantly phytophagous diet for _Trichocorixella mexicana_ , but Sokol'skaya and Zhiteneva (1973) found _Sigara_ and _Cymatia_ species to be predatory, attacking fish fry.

This dichotomy of views between the herbivorous and carnivorous modes of life for corixids still continues in the more general literature. Cobben and Pillot (1960), Popham (1959, 1964), Parsons (1966) and Fernando (1959) saw corixids as chiefly herbivorous, with references to carnivory considered as rather special cases, although Martin (1970) and Pajunen (1970) both described corixids as important predators in small ponds. Brooks and Kelton (1967) and Istock (1973), almost alone, take a more "omnivorous" viewpoint, although the latter stated that no good information as yet existed for any species on diet.

The whole history of research on corixid feeding contains a series of generalisations based on studies of a few species in one area with extrapolation to other species through similarities in habitat and morphology, as pointed out more generally by Cummins (1973). It might be truer to say that corixid species are generally opportunist feeders, some highly carnivorous and others tending towards microphagy. Palar modifications may not be easy to ascribe to function; thus, despite their very different palar shapes, both _C. americana_ and _Glaenocorisa_ are powerful swimmers and predators (Walton, 1943

b). Sutton (1951) describes the varied uses of the palae; to hold prey, winnow debris and create water curents. Such diversity would likely preclude specialisation in cne direction. Both Walton and Sutton (_op_. _cit_.) observed capture and feeding upon live prey.

According to Macan (1962) "corixids rarely ccntain anything identifiable, and attempts to study their food have led nowhere". Gut examination (Walton, 1943 b; Suttcn, 1947a; Fernando, 1959) usually reveals a mass of unidentified brownish or greenish material with some recognisable diatoms. These may come from the alimentary tract of a prey organism, but it is likely that they are also ingested directly. Thus feeding hatits can best be established through other means of dietary study, such as using radio-active tracers (James, 1960) or serological means (see the next Chapter), through rearing experiments or through feeding selected fcodstuffs.

Despite the views of Hungerford and Griffith (_op_. _cit_.) there is only one example of successful rearing thrcugh several consecutive generations on wholly plant material; that of Peters and Ulbrich (1973) who reported that _Trichocorixella_ _mexicana_ could be reared on autoclaved mud plus branched algae. These authors also frequently added _Tubifex_ to other rearing cultures. Jansson and Scudder (1972) have reared _Cenocorixa_ species using both live and frozen brine shrimp, while Peters (1962) used _Elodea_, algae and tubificids to rear ten successive generations of _Krisousacorixa_ _femorata_. It is likely that there is a need for some animal food, perhaps to ensure successful reprcduction.

Zwart (1965) suggested that most forms of animal food were adequate for corixid reproduction. This animal protein need was also suggested by Pajunen (1970a), who said that in captivity female corixids would suck their eggs at a level correlated with food lack. The same habit has been observed here for Cenocorixa.

In the present study C. bifida and C. expleta were tested in feeding experiments with as many foodstuffs, plant and animal, as could commonly be found in the littoral of the lakes studied, to assess the potential feeding range of these species under experimental conditions. Results demonstrated a primarily carnivorous nature for both Cenocorixa species. Difficulty was experienced in observing the response of corixids to algae and higher plants, as a determined movement towards a plant resting place might appear similar to a feeding attack on an animal prey. However, the rapid leg-beating of a feeding corixid was unmistakeable.

The ooze and algal feeding pattern so frequently associated with corixids (i.e. Hungerford, 1919) was seen occasionally; one sample of corixids collected in fall of 1973 in Lake LB 2 contained several adults whose guts were filled with a bright blue-green substance, probably cyanophyte material. Also, adults offered periphyton later left greyish-green faecal material which might have been algal, and several guts examined contained recognisable diatoms. The possibility also exists that these may have come from the guts of prey organisms.

It was observed that early instars usually picked over the bottom of the test dish, and adults often systematically probed

with their mouthparts the plastic screening provided for them to cling to, square by square, as if searching for food. Many reports of corixids feeding on aquatic macrophytes are suspected to be in fact the probing of the surface for small invertebrates in a similar manner. Eggs of _Enallagma_ species, the common genus of damsel-fly in the studied lakes, are inserted into slits in submerged vegetation, and feeding might be upon material such as this rather than on the plants themselves.

Evidence of carnivory was more concrete; both species seemed to prefer dead foods to live, perhaps being connected with a limited ability to capture some prey. Planktonic organisms and chironomid larvae comprised the major food items. Only a few organisms were ignored, among these being hydracarina. These may be distasteful to corixids, as they appear to be to many predators (Frost and Smyly, 1952). Elton (1923) suggests that this may be partly a response to their red colour, but feeding on red diaptomids would seem to refute this.

As well as demonstrating carnivory, evidence was obtained of a predatory habit, both in feeding results and in the increased interest evinced by a corixid in a moving prey organism. It appears that detection of motion need not be by vision alone, as even prey behind the corixid were detected and captured, suggesting that the corixids as a group are sensitive to pressure changes in the water. Dahm (1972) noted that underwater vibrations were important stimuli for the related hemipteran _Notonecta_ to locate their prey, and these consistently responded to irregular motion of models through the

water. Light and vision conditions did not affect nctcnectid prey capture success, but this was lowered by the presence of dense aquatic vegetation, or by constant disturbance of the water surface. Murphey (1971) also showed that Gerridae similarly responded to water disturbances, through leg sensors. Thus the related corixid group may also rely heavily cn pressure detection to locate prey at a distance.

In the experimental situation used, one major prcblem seemed to lie in the difficulty of corixids in initially discovering their prey organisms; reflections from the container walls possibly adding to problems of orientation. The presence of a piece of screening in the bottom of each container prcvided some degree of heterogeneity and an area for the corixid to cling to, but it also acted as a camouflage for some types of prey, and its removal at the end of the experiment often triggered rapid predation on previously ignored prey.

Once a prey organism is captured and subdued, perhaps ky injection of the venomous maxillary gland secreticns referred to earlier, its body juices are rapidly sucked out by the action of the pharangeal pump. This structure has been linked with carnivory and the predatory habit, but Hungerford (1917a) has shown that certain corixids will pierce individual cells of a filamentous green alga, and suck out the contents. Further evidence for a mixed feeding habit including phytcphagy and detritus-eating has been adduced from the presence of teeth in the pharangeal pump, considered to be present tc comminute or strain out the larger ingested solids (Slack, 1947; Parsons,

1957b).

Reports of a peritrophic membrane in the corixid gut (Sutton, 1951) are apparently related to the presence of solid food particles. Parsons (1957a) investigated North American species of Sigara, Trichocorixa and Hesperocorixa. Histological sections through the midgut often showed fragments of crustacean exoskeleton within the foodmass; these may be identified by the bristles, and by reacting with a test specific for chitosan.

In one feeding experiment, a corixid fed a gravid Daphnia was found to have several whole daphniid embryos in the gut, as the stylet canal is wide enough to allow solids to pass through (Parsons, 1957a). Also in the present study and in other observations (i.e. Hungerford, 1948) diatoms were seen in the gut. However, it is possible that these might have come from the alimentary system of a herbivorous prey such as an ephemeropteran or a chironomid.

Feeding on red chironomids usually resulted in a deep red colour to the midgut, visible in juveniles through the body wall. This colour rarely persisted to the hindgut region, digestion rapidly converting the haemoglobins to a brownish mass. On the other hand, orange-pink fatty droplets coloured with carotenoids from diaptomid foods were sometimes seen at the corixid anus, so that this food could be detected at a later stage in the feeding process. Red guts were seen in field-collected samples from first instar to adult, suggesting diaptomid food at all stages of each species. Jansson (1971) and Jansson and Scudder (1974) also mentioned the appearance of red

guts in field-collected corixids of all instars, and suggest
that this represents feeding on _Diaptomus sicilis_ , alive or
dead. In the literature, a greenish or brownish gut has often
been correlated with algal feeding (Griffith, 1945; Fernando,
1959); this colour was seen occasionally in field-collected
corixids in the present study (see Chapter V) but was not
recorded in feeding experiments.

Given abundant foods, corixids frequently abandoned half-
eaten prey for other live ones. These observations parallel
laboratory experiments with Gerridae fed excess prey (Jamieson,
1973). Jamieson suggests that such a situation would be rare in
the field. However, on Becher's Prairie excess prey might have
been frequently encountered, in the form of synchronous
emergence of chironomids, or of plankton swarms inshore. Prey
choice experiments indicated that plankters elicited the
strongest predatory reactions, despite a relatively low capture
success. The feeding habit of _Cenocorixa_ taking both live and
dead prey could have added significance in this light, since
temporary plankton blooms or inshore drifts could be exploited
while live, and the excess killed and partly eaten would provide
food for later periods as well as feeding smaller instars which
show the most pronounced preference for dead foodstuffs.

The single prey feeding experiments indicated differences
in specific food preference and in feeding response to prey
offered, by sexes, instars and species of _Cenocorixa_ . In the
main, late instars were most voracious, adults occupied an
intermediate position while instars one to three fed least

heavily. This reflects the fact that the fourth and fifth instars are the periods of most rapid growth and development of adult body structures, and consequently maximal food intake is needed.

The pattern possibly also reflects heterogeneity among adults in reproductive stage, linked to feeding intensity. Young adult corixids may need to feed heavily in the teneral period, when egg maturation is continuing; the level of 67.4% feeding with 92 tenerals tested is high in comparison with the mean feeding intensity of all forms. Once the adult excskeleton is fully hardened, it is impossible to distinguish externally whether the corixid is at the height of oviposition or is spent. Reduced feeding might occur in the latter state, but no method was devised to test the results for any bias that might be thus introduced.

Overall, C. bifida showed a slight preference for live food over dead. However, C. expleta fairly consistently preferred most types of prey dead to live; this constitutes a distinct biological difference between the species at least in the context of the experiments, and ignoring in the main the effects of different life stages. Tests showed consistently, if non-significantly, greater feeding by C. expleta than C. bifida on dead chironomids, dead daphniids, dead amphipods and dead zygopterans On the other hand, C. bifida fed more than C. expleta on live small plankters.

The low activity score recorded for both species of Cenocorixa with chaoborid larvae as prey may in part be due to

the habit of the latter of floating motionless near the surface in experiments. To C. expleta from Lake LB 2, where chaoborid have not been recorded, the prey may to some extent resemble Branchinecta and evoke similar feeding responses. Test scores for feeding on both foods were almost equal and, although these prey sometimes differ in size, both have a similar lack of colour, hang horizontal or slightly inclined in the water, and show rather similar escape movements when approached.

Feeding pattern, as shown by feeding experiments, differed less between the juvenile stages than between adults of each species. Feeding habits tended to differ more between conspecifics of different instars than between species of the same instar; this is probably largely a factor of the food available to, and easily capturable by, each size-range of corixid juveniles.

In mixed prey experiments, species differences were again seen. Thus, when offered mixed plankton, C. bifida selected daphniids whether live or dead, whereas C. expleta seemed to take both diaptomids and daphniids in the proportions offered. Initial considerations suggested that this result might be related to the differing proportions of plankters inshore, where C. bifida predominates, compared to openwater habitats where C. expleta is proportionately more abundant. However, midlake plankton hauls suggested that diaptomids may be less frequent there than inshore. Perhaps C. expleta may show superior mobility and predatory success; its equivalent instars are larger than those of C. bifida , and may be more efficient at

capturing their prey.

In other mixed prey experiments, both species behaved similarly, preferring chironomid over planktonic organisms and taking zygopteran relatively rarely. However, unsuccessful attacks were made most often on daphniids, and there was no significant difference between those made on the chironomid and zygopteran prey offered, both being much fewer. Results thus strongly uphold the ideas that corixids are first alerted to prey presence by motion, which would be more frequent in a continuously swimming plankter than in the relatively immobile benthic and littoral organisms. Also, Cenocorixa species appear to be relatively inefficient predators, for although showing a typically predatory response to prey movement, they are frequently unsuccessful in its capture.

Despite the demonstrated dietary preferences, it appears that a wide range of food, live or dead but predominantly animal, may be accepted by Cenocorixa , and possibly the sympatric H. laevigata , in the field. Feeding experiments showed no cannibalism, but in preliminary tests there were many attacks on early instars by starved corixids of both species, and several juveniles were found dead, apparently pierced through the head region and sucked. Many Cenocorixa in captivity carried out a systematic search of the plastic screening in the test dish, and sucked any of their eggs thus encountered. Other species have also been recorded to suck their own eggs in captivity (Sailer, 1948; Crisp, 1962 b; Pajunen, 1970a) while C. americana species will eat its own nymphs, even in the first

instar (Hungerford, 1923; Walton, 1943 b). These behaviour patterns in corixids need more study, but they represent in most forms probably a feeding habit resorted to in times of stress or inadequate food.

In summary, results of feeding experiments point to a predominance of carnivory and some predation as a food pattern for Cenocorixa . Species differences within the genus were not marked, although C. expleta tended to prefer dead foods to live, and the reverse pattern was seen in C. bifida . Thus it would seem that, with regard to feeding pattern, fundamental niches of the two species are similar in range, although not identical in details.

CHAPTER V. SEROLOGICAL INVESTIGATIONS OF GUT CONTENTS

INTRODUCTION

The potential of the immune response as a biological tool was recognised early, and while in use routinely in medicine for 'immunisation' its _in_ _vitro_ properties were also being studied (Crowle, 1961). It has often been called the 'precipitin reaction' because of the visible results of mixing, layering or allowing to diffuse together, an antigen and its corresponding antibody. Thus the precipitation seen becomes diagnostic for the presence or absence of the antigen, due to the specific nature of the reaction.

Orlowski _et_ _al_. (1972) used the technique to separate the visually identical eggs of two closely related species of rockfish, and its use in taxonomic problems is widespread (i.e. Basford _et_ _al_., 1968; Leone, 1947), even at the intraspecific level (Ridgway _et_ _al_., 1962). The technique has even been used to follow physiological-morphological development in animals, based on the fact that juvenile globulins differ from those in adults (Koeppe and Gilbert, 1973; Telfer and Williams, 1953).

The usefulness of the precipitin reaction to identify blood meals of economically important insect pests has been recognised for a long time, and since Nuttall (1904) it has been used in feeding studies of mosquitoes (e.g. Bull and King, 1923; Riddell _et_ _al_., 1947; Eligh, 1952; Edman _et_ _al_., 1972), blackflies

(Downe and Morrison, 1957) and <u>Glossina</u> (Emslie and Steinberg, 1973). The method involves preparing antibody sera specific to different postulated mammalian and avian hosts, and testing the gut contents of the flies for positive precipitin reactions with these.

Somewhat later, the method was recognised as being potentially useful for many other predator-prey relationships where direct analysis of gut contents or observations of feeding pattern were not possible. Thus Brooke and Proske (1946) and Service (1973) determined the important insect predators of juvenile mosquitoes using the precipitin test. Sergeeva (1970) studied predation on <u>Eurygaster</u> species using this technique, as did Sutton (1970) on woodlice.

The technique has also been used by Dempster (1958, 1960, 1963; Dempster <u>et al</u>., 1959) to study the predators of broom beetles, <u>Phytodecta</u>, and by Fox and Maclellan (1956) in their study of carabid predation. Finally, Frank (1967, 1971) has studied the feeding of a variety of organisms by this technique, and it has been utilised in studies on the feeding relationships of British triclads (Young <u>et al</u>., 1964; Davies, 1969; Pickavance, 1970; Reynoldson and Davies, 1970; Reynoldson and Bellamy, 1973). West (1950) and Hall <u>et al</u>. (1953) have discussed the precipitin test with regard to general insect predator-prey relationships .

Reactant sera can be produced in response to plant antigens as well as to those of animal origin. Bernhard <u>et al</u>. (1969) used an immunofluorescence technique to separate groups of

phytoplankters, although specificity of the sera was not high. Gell et al. (1960) studied the taxonomy of Solanum species using the precipitin test, and by the same technique Ueckert and Hanson (1971) investigated dietary overlap in grasshoppers. Medical understanding of allergies involves the use of immune tests, as most allergies depend on the sensitising of the patient to plant allergens (antigens), often carried in pollens. Thus Bernstein and Safferman (1973) showed clinical sensitivity to green algae in vitro, and Weber (1973) reviewed recent studies involving immune reactions to plants.

The history of the technique's development consists essentially of its refinement and miniaturisation, and in developing suitable staining or fluorescent methods to make the precipitate readily visible. Pickavance (1970) has ably summarised most major steps in the development of the technique and presented an empirical formulation of the most satisfactory methods. It is his technique which, minor modifications, was followed in this study.

The food taken by the two species of Cenocorixa in nature was assessed by a serological investigation of the gut contents of each species in allopatry and sympatry. In this way it was hoped to obtain a measure of the realised niches of each species.

METHODS

Preparation of slides and templates

Methods for serological examination of field-collected corixid guts were taken mainly from Pickavance (1970). The process adopted, incorporating those modifications found necessary, was as follows.

Numbered slides (2.5 by 7.5 cm) were boiled in a slide rack in weak detergent for 15 minutes, rinsed for 15 minutes under running tap water and then in three changes of distilled water, and drained. The cleaned slides were then sluiced in hot 0.2% 'Difco' Bacto-agar dissolved in distilled water, then drained and dried in a dust-free place on absorbent paper towelling. The thin agar film served as a cement for the agar gel layer that was applied later. At this stage, slides could be stored indefinitely, if air was permitted to circulate between them.

When needed for use, a number (about ten) of slides were placed with numbers oriented and edges opposing, and two layers of 1.9 cm Scotch Vinyl plastic electric tape, each 0.35 mm thick, applied so as to enclose a central area on each slide about 2.5 cm square and 0.7 mm deep, in which the gels were to be placed. The layers of tape were applied closer to the bottom edge of the slide than to the numbered edge for rapid orientation. Masking tape, initially used for one border to simplify orientation, was not further used after initial tests confirmed the observations by Proom (1943) that this may interfere with the serological reactions.

Ouchterlony templates were cut from 3 mm thick perspex sheeting. Eight 1.2 mm holes were drilled through each 5.5 cm diameter disc around a central hole of the same size, and 0.5 cm distant from it; the nine hole cluster thus occupied a central position one cm in diameter. All holes were then partly redrilled to a depth of 2 mm using a 3 mm bit, to produce a funnel (figure 17).

The final plates were then assembled as follows. An agar-coated, taped slide was warmed slightly on a 37 C hotplate. Then 0.2 ml of molten 1% 'Difco' Bacto-agar made up in 0.9% saline solution was pipetted onto the centre of the slide and an Ouchterlony plate lowered gently onto it. The tapes allowed the agar to flow out to give a layer of uniform thickness, with the funnels of the Ouchterlony plate in direct contact with the surface. Occasionally molten agar welled up into the funnels when the agar was not hot enough; or air bubbles were trapped or air was drawn through the funnels by the shrinkage of the solidifying agar, leaving an air space beneath the Ouchterlony plate. Such slide assemblages were discarded. Others were placed in a saturated humidity environment for about one hour to harden - it was found convenient to use a three litre plastic container with a tight-fitting lid, and lined with filter paper soaked in distilled water. Fungal growth occurred occasionally in this environment as tests were run for 48 h at room temperatures; fungi grew more prolifically if paper towelling was used in place of filter paper.

Figure 17. Details of serological technique.

A: preparation of the Ouchterlony plate.

B: arrangement of antisera in disc funnels as used in tests.

C: Diagram of finished slide, showing adjacent stained precipitin bands.

A

funnel
(section)

template

double layer
tape

J 90

agar

B

Diaptomus

Zygoptera   Chaoborus

TEST
GUT

Various   Amphipoda

Ephemeridae   Chironomidae

Daphnia

C

J 90

reaction bands
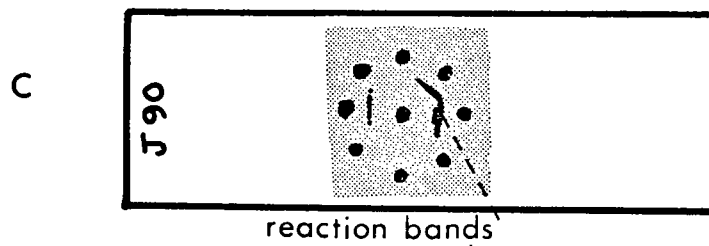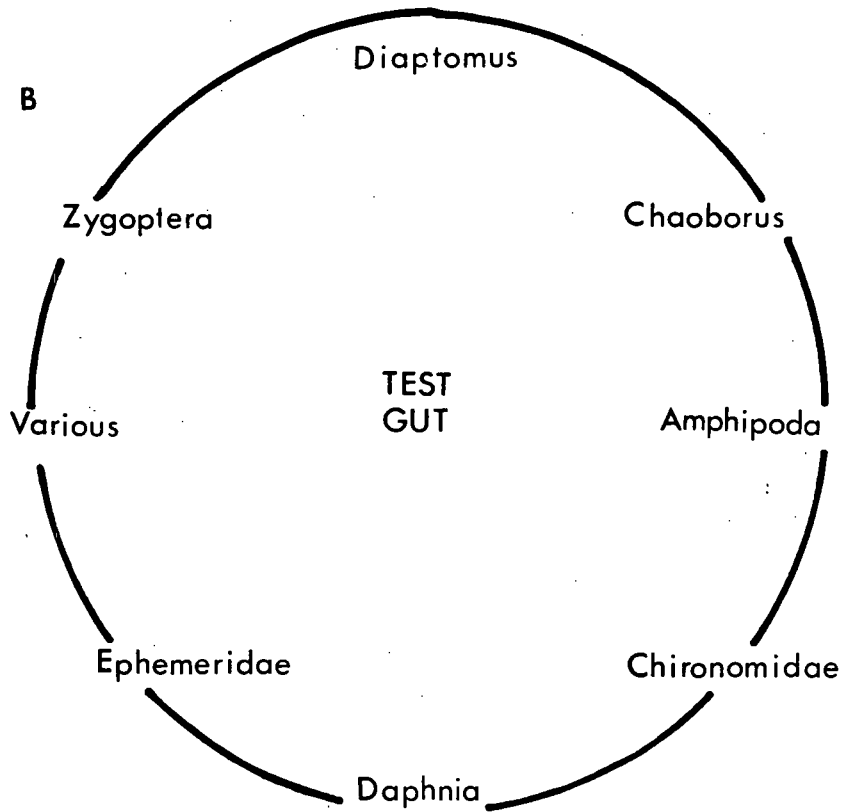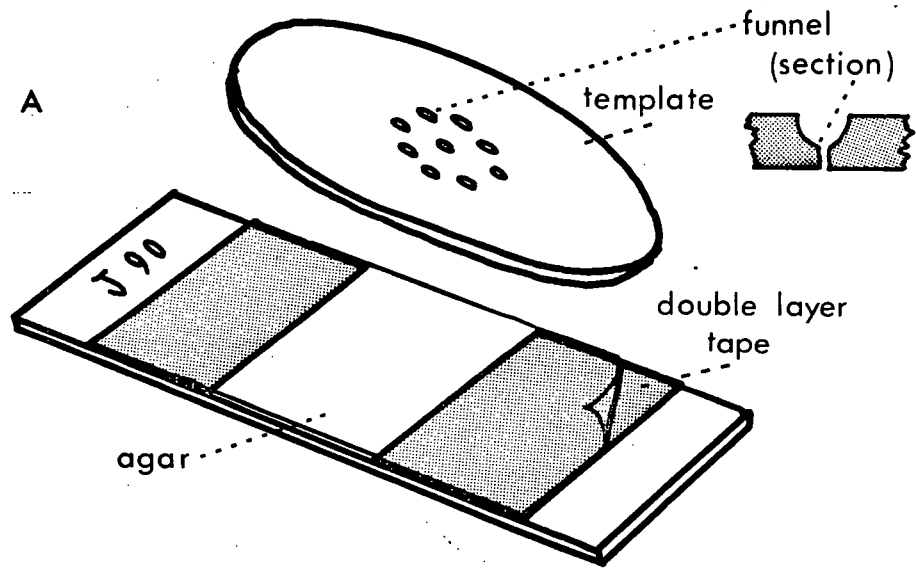
Preparation of antigens

Based on observations and experiments on the feeding pattern of <u>Cenocorixa</u> species, reported in Chapter IV, and on the organisms present in some abundance in the experimental lakes (chapter II), eleven groups of potential prey organisms were used in the preparation of antigens for antiseral production (Table XXVI). All organisms were collected with a net, sorted to component groups and starved of food for three to five days in filtered water from their own environments. This water was changed several times during starvation. Pickavance (1970) starved organisms for seven days to rid the gut of foreign proteins, which might have produced non-specific reactions, but Young <u>et al</u>. (1964) used a four to five day starvation period. Living specimens were then blotted dry and quick-frozen on dry ice in 1 - 4 ml aliquots in small 'Nalgene' plastic tubes, then stored in a deep-freeze at -20 C.

Most organisms were collected in summer, 1972, at the Becher's Prairie field-site, but some had to be supplemented from other sources, namely Lakes Eunice and Marion in the U.B.C. Research Forest near Haney, and ditches in the U.B.C. Endowment Lands, along Wesbrook Crescent and 16th Avenue. Details of prey organisms and their collection sites are listed in Table XXVI.

The collected animals were later unfrozen and 1 ml aliquots homogenised with equal volumes of 0.9 % saline for 5 - 10 minutes using a ground-glass pestle and mortar with effective capacity of about 5 ml, kept semi-immersed in crushed ice to

Table XXVI. Potential prey organisms used to produce antisera in order of their abundance within each group, with areas of origin.

	ANTIGEN ORIGIN	DETAILS
1:	DIAPTOMIDS	*Diaptomus nevadensis* (Round-up, Lye) *D. sicilis* (Barnes, Round-up, Lye, LB 2) *D. kenae* (Eunice L., U.B.C. Research Forest) *D. caducus* (U.B.C. Campus)
2:	DAPHNIIDS	*Daphnia magna* (Rock, East) *D. pulex, D. schodleri* (Lye, Round-up) *D. similis, Ceriodaphnia* sp. (Barnes)
3:	AMPHIPODS	*Hyalella azteca* (Greer, Rock, East, Marion) *Gammarus lacustris* (Greer, Rock, East)
4:	CHAOBORUS	*Chaoborus americanus* (East, Eunice) *C. nyablei* (Eunice)
5:	CHIRONOMIDS	*Einfeldia pagana, Glyptotendipes barbipes* (all Becher's Prairie lakes) *Derotanypus alaskensis* (Lye) *Procladius clavus, Chironomus* sp. (Barnes) Chironomini (Marion)
6:	EPHEMEROPTERANS	*Callibaetis* sp. (Barnes, Round-up, Lye, Greer).
7:	ZYGOPTERANS	*Enallagma* sp. (all Becher's Prairie lakes and U.B.C. Campus).
8:	PULMONATES	Planorbidae (Rock, Greer, East) Lymnaeidae (Marion, U.b.c. campus)
9:	BLUE-GREEN ALGAE	Unidentified, forms dense blooms, (East).
10:	GREEN ALGAE	*Cladophora* and *Spirogyra* spp. And other filamentous forms (Rock, Greer)
11:	MACROPHYTES	*Potamogeton pusillus, Ceratophyllum demersum, Myriophyllum spicatum* *Ruppia maritima* (Greer, Rock, East)

prevent heat denaturation of proteins. The homogenate was then pipetted into tubes and deep-frozen. All homogenates for one group of potential food organisms were then combined and centrifuged at 9000 rpm for 15 minutes in a refrigerating ultracentrifuge. The clear supernatant containing the desired antigenic proteins was then decanted and stored in 1 ml portions at -20 C until required for injection. Pickavance (1970) found that this procedure should yield 1% to 5% protein, depending upon prey source, and adequate to initiate antibody production. Davies (1969) used 'a few ml' of 0.9% saline, and this greater dilution gave a soluble protein level of 0.85% to 1.25% protein, while Young et al. (1964) used a 'small volume' of saline to get a protein concentration of 0.4%. The present protein levels were considered to lie within Pickavance's levels, although no Biuret protein estimates were made.

Preparation of anti-sera

Young adult New Zealand rabbits were kept in outside cages at the U.B.C. Vivarium, and fed a standard diet, from which antibiotics were absent to minimise immunological interference. After one week's acclimatisation the rabbits were test-bled to check for any pre-existing antigens which might interfere with the reactions. Rabbits were hand-held in their normal posture during all bleeding and immunisation procedures.

Before test-bleeding the ear was shaved and lightly swabbed

with xylol to increase blood flow. Although ambient temperatures were close to freezing at the time, there was a dramatic increase in ear temperature and dilation of blood vessels in the ear. The marginal vein was then nicked and 1 to 3 ml of blood collected in a tube, which was then lightly capped with 'Parafilm'. Treatment of blood samples is described below. A patch of skin about two inches square was then shaved low down on the right flank to facilitate inoculation. Injections were given subcutaneously following Pickavance (1970), although Fink and Quin (1953) reported best results with intra-abdominal injections.

After four days, during which the test-bleeding was checked, the shaved flank was swabbed with alcohol and one ml of antigen was injected subcutaneously using a 1 ml 'Tomac' disposable syringe with a number 21 or 27 needle ; the latter was preferred as its small size made injection less difficult. Four injections of 1 ml antigen each were given at four-day intervals. Rabbits were then left for 21 days to build up anti-bodies, as Pickavance (1970) indicated that, despite controversy in the literature, the antibody titre usually peaked after that period.

Seven days after the final injection rabbits were again test-bled to check for antibody titre levels. The final bleeding differed from the test procedures as both ears were shaved and swabbed with xylol. Marginal veins were then sliced across and blood collected in 12 ml centrifuge tubes. Usually about 10 ml could be collected from one incision before reduced blood flow

or clotting necessitated a further incision. In all, about 30 to 40 ml of blood was collected from each rabbit, a process that took about half an hour. Rabbits were then checked to see that bleeding had ceased, and returned to their cages.

The tops of centrifuge tubes containing blood were covered with parafilm. Pickavance (1970) suggested that the blood should be allowed to stand over night, then centrifuged and the serum pipetted off and frozen. However, extensive haemolysis was often observed when this was attempted. This phenomenon is common with rabbit blood (Ms. J. Hards, personal communication) and might have been due to xylol fumes, the abrupt changes of temperature unavoidable when working out of doors in winter, or a number of other causes. Although not critical in relation to the precipitin test itself, it was detrimental to the operation of some antiserum titre tests (see below). The standing period was thus reduced to shorter periods (under six hours) of clotting at laboratory temperatures; clots were then gently loosened from the edge of the centrifuge tubes to minimise their rupture, and any supernatant present carefully pipetted off. The blood was then lightly centrifuged in a BHG Roto-Uni centrifuge at 2000 to 2500 rpm for about 5 minutes to compress the clots and release pockets of serum. The serum was drawn off and stored at -20 C.

In some cases antibody production was insufficient. Rabbits were therefore re-injected with two weekly booster shots each of 1 ml containing antigen emulsified volume per volume with Freund's complete Bacto-Adjuvant (Difco Chemicals), and bled seven days after the second injection. The booster schedule was

arranged differently, since a more rapid rise occurred in
antibody titre than with original immunisation (Pickavance,
1970). According to most authors (i.e. Jurin and Tannock, 1972)
Freund's adjuvant has properties of intensifying and spreading
the specificity of the antigen reaction. It also has less well
publicised side effects, causing apparent pain on injection
(this was not observed when antigens alone were injected) and
frequently producing a reaction at the injection site, either as
as open sore or a hard lump under the skin. For these reasons it
was not at first used. However, results produced only weak sera
except with chaoborid antigen, so adjuvant booster shots were
necessary in the preparation of all other antisera.

The serological tests

Two methods of serological gut study were investigated
before a decision was taken to follow the method of Pickavance
(1970). Many authors have followed the method of Bull and King,
who smeared gut contents in the field onto filter paper and
allowed it to dry, then stored it in a dessicator (i.e. Sutton,
1970), or deep-frozen (i.e. Davies, 1969). In a variant of this
technique, Downe and Morrison (1957) report the use of guts from
dried, pinned insect specimens. The smear method using filter
paper was attempted using guts of starved corixids and of those
fed diaptomids and chironomids, but following reconstitution of
the smear with 0.9% saline and testing it against antisera on an
Ouchterlony plate, as described below, no positive results of

feeding were obtained, although parallel experiments using guts frozen instead of dried produced the serological reactions expected. With the availability of dry ice and deep-freeze facilities near the study area the filter paper smear technique was not investigated further.

Immunological reactions were also looked at following the methods in Davies (1969), who used the Morris (1964) version of Preer's (1956) modified Oakley-Fulthorpe method; this method was earlier used by Bull and King (1923) to test mosquito meals. The technique involved coating the inside of 4 cm lengths of 2 mm glass tubing with 0.1 % agar dissolved in distilled water, and leaving these to dry. A 6 mm column of hot agar plus buffer was then pipetted into the centre, and equal volumes of antiserum and test antigen layered on either end. The tube ends were then sealed with parafilm and the tube incubated at room temperature for three days. Difficulties were encountered in centralising the median agar plug and in layering the reagents onto this without trapping air bubbles. Fungal contamination also affected a small proportion of the tests. Although precipitin rings formed in most tests satisfactorily, the method was not continued as it was time-consuming, used large volumes of reagents and could not test more than one antiserum at one time. Therefore the Pickavance (1970) method was followed in all testing of the corixids.

Corixid samples were unfrozen and placed on a clean glass plate for microscopic identification. The abdomen of each was dissected from the thorax and the gut removed and macerated in a

drop of 0.9% saline. The resulting fluid was pipetted into the central funnel of an assembled plate, while the peripheral funnels were filled with anti-sera, arranged in a standard pattern (figure 17).

Funnels were filled using disposable 5 lamda (microliter) micropipettes (Drummond Microcaps): with coarser pipettes trapped air-bubbles often prevented the reagents from reaching the agar surface. Plates when so set up were left in a saturated environment to incubate for 48 h so as to ensure complete precipitation, although the reaction was noted to be well advanced in a few hours. Tests were usually run with 24 or 36 slides simultaneously, taking one to two hours to set up.

After 48 hours the Ouchterlony plates were snapped off the gels and the tapes peeled off. To leech out unprecipitated proteins the slides were then soaked overnight in a physiologic sodium phosphate buffer at pH 7.4, prepared using Gomori's method (Humason, 1966, p.502). For this, stock solutions of monobasic and dibasic sodium phosphate were mixed in the ratio of 19 : 81 to give the correct pH, and made up to a 0.1 M solution.

Slides were then removed from the buffer and steeped in two changes of distilled water for about ten minutes in each. They were then soaked for exactly ten minutes in a protein stain, then destained in three baths of 1% acetic acid until the gels were clear or only faintly pink, and the precipitate bands stood out as brightly coloured arcs. A red stain allowed direct projection of the slide onto grade 3 bromide paper, as shown in

Figures 18 and 19. Acid fuchsin in 1% acetic acid was initially used, but Thiazine red was found to give a superior colour. Slides were then dried at room temperature in a dust-free place. This caused the gels to shrink to a fraction of their original thickness and to become permanent mounts, withstanding indefinite storage.

Slides were examined by eye, and all precipitin bands noted. Results of the tests were analysed using a computer programme written by Ms. Dolores Lauriente, which subdivided the data by food item, species, instar, lake group and season. In all, 1872 tests of gut contents which yielded valid results were used in computations.

One problem involved bonding of the agar gel to the slide base. In certain batches of slides the gels floated off the slides at some stage in the staining process. Several things seemed to account for this; repeated washing during staining may be a minor causal factor. However, it is likely that floating off of the agar gels is chiefly caused by bacterial action, since in cases where corixid samples were left unfrozen for some hours before testing, gels subsequently floated off at a rate of nearly one in three. Unless the gel was detected before it had shifted appreciably, the test had to be discarded as its orientation was lost.

Figure 18. Results of some serological experiments, showing typical precipitin band patterns.

A: 3 contiguous bands (amphipods, chironomids, daphniids).

B: 4 bands (chironomids, ephmeropterans, daphniids, zygopterans).

C: four contiguous bands.

D: Strong reaction with daphniid, weak with amphipod antisera.

E,F,G: two double bands at different loci.

G: Strong band for chironomids; no band for zygopterans.

I: Bands close to radial funnel positions.

(A-D,G,H: note deposition of suspended material around funnel openings).
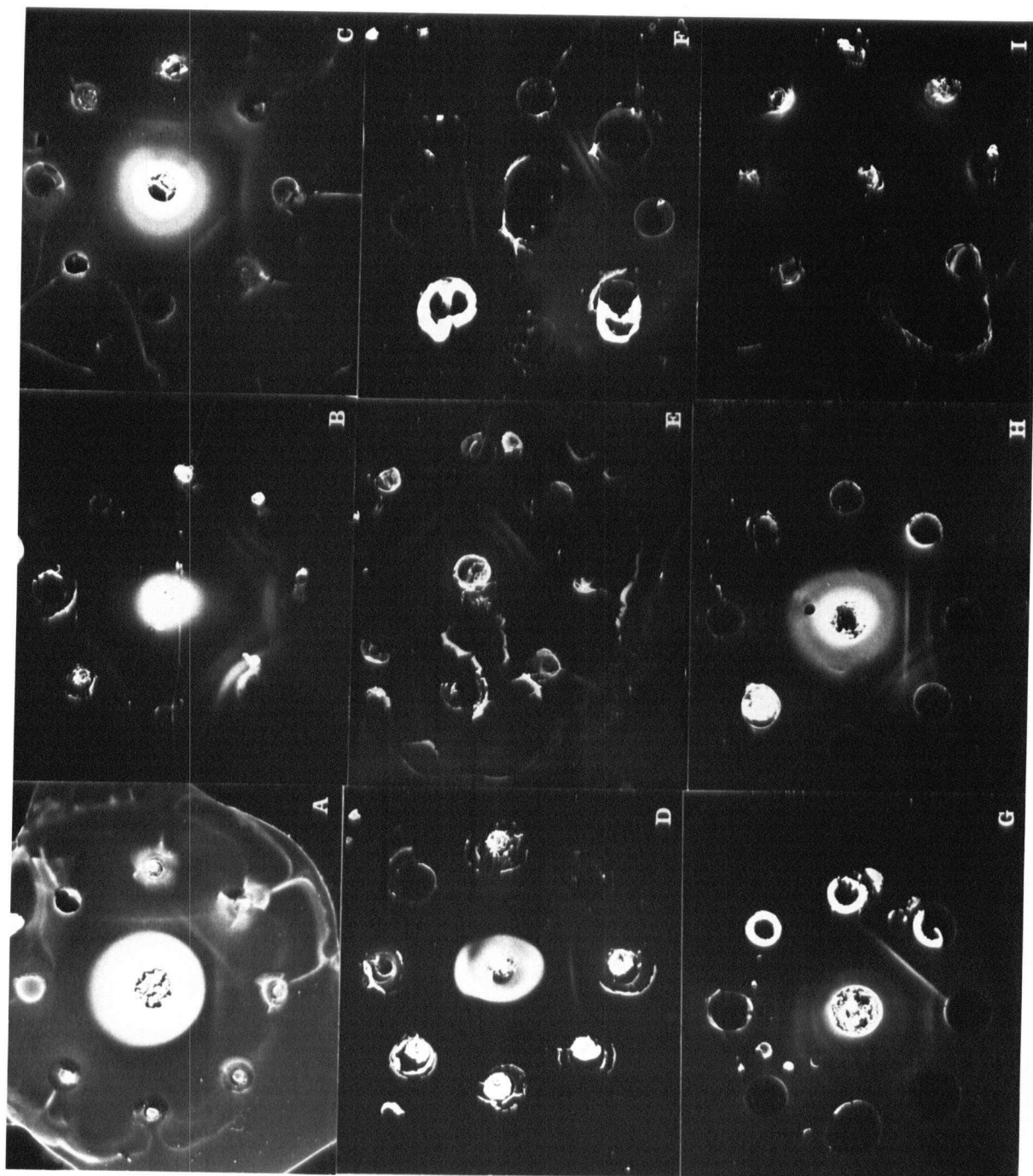
Figure 19. Results of some serological experiments, showing typical precipitin band patterns.

A: single band for amphipods.

B: Single band for diaptomids.

C: Single band for zygopterans (no reaction for chironomids).

D: single reaction with ephemeropterans (double band).

E: Single band for daphniids.

F: single reaction for chironomids (multiple band).

G,H: different configurations of contiguous reactions with daphniids and chironomids.

I: single reaction with chironomids (single band; compare with 'f').
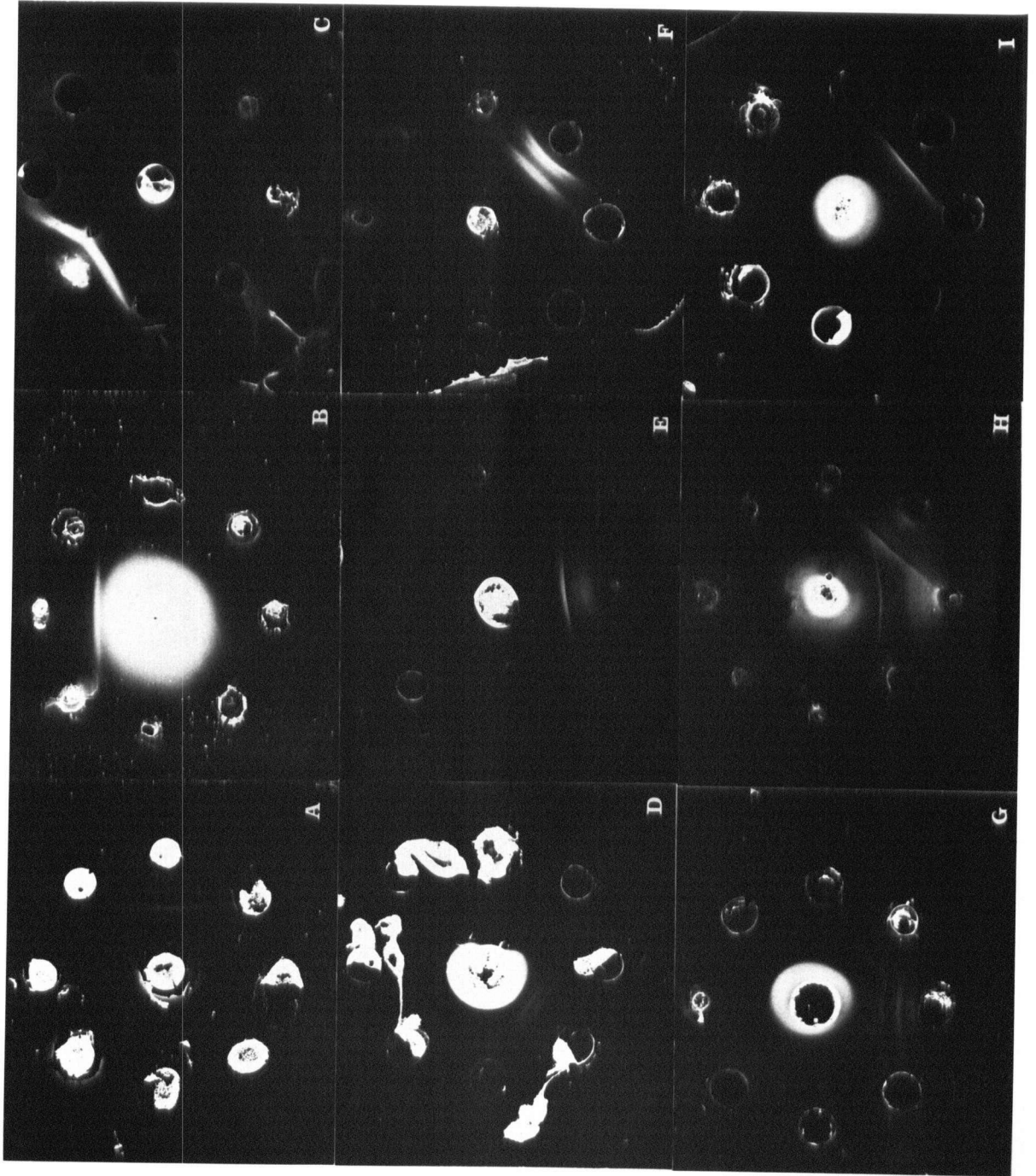
Tests of the serological method

The accuracy of the serological techniques used in this study was checked in several ways. Specificity of each anti-serum was most important; other tests involved isolating fed and starved corixids for varying lengths of time to estimate how long food remained detectable in the gut, and attempts to judge the relative sensitivity or strength of the antisera.

(i) Specificity of the antisera

Sera were tested on three occasions. First, rabbits were checked before inoculations commenced, for any pre-existing antibodies that would react with the antigens to be injected. Results were uniformly negative. Then, seven days after the final injection, test-bleedings were checked against the range of antigens to look for an increase in antibody titre. At this stage most sera gave weak but positive reactions. After 21 days the final bleedings were performed and sera tested against the full range of antigens. Of these, aquatic macrophyte antiserum alone produced no positive reactions. Filamentous green alga antiserum gave a faint but specific reaction, and others were considerably stronger.

The 21 day sera were specific for chaoborids, zygopterans, ephemeropterans, daphniids, diaptomids and snails. One of two tests of the chironomid antiserum showed a faint reaction with

zygopteran antigen, while one of four tests of the amphipod antiserum showed a similar faint reaction also with daphniid antigen. The latter is suspected to be a result of accidental contamination of test plates, and was not recorded subsequently. However, the faint zygopteran band using chironomid antiserum was more of a problem as these, the dominant corixid foodstuffs, often co-occurred in test results.

Tests were also run using unstarved whole prey organisms in place of purified antigenic solutions, versus a range of antisera. These tests gave equivocal results, for although both replicates with diaptomids were specific, one of six replicates with chironomids showed a faint reaction with zygopteran antiserum in addition to showing strong chironomid specificity. Three chaoborid replicates gave strong responses with chaoborid antiserum and weak ones with daphniid, diaptomid and chironomid antisera, probably typical dietary constituents of these forms.

The faint reactions of some chironomid tests with zygopteran antiserum, and vice versa, were puzzling as they appeared in a few tests only (see Figures 18G, 19C). The single reaction of chironomids with zygopteran antiserum which appeared in tests with unstarved forms might indicate tendipedid predation on zygopteran eggs or very young nymphs. To explain the occasionally seen reverse reaction, it is possible that the zygopterans collected for antigen production were not adequately starved and that some chironomids as prey persisted in their guts.

Many guts of wild-caught corixids showed a reaction with

only one of these two antisera, zygopteran and chironomid, although others reacted with both, which might be expected in the wild. Since the single reaction band was often intense, this indicated that cross-reactions probably played no or at most a negligible part in the actual tests. Thus, absorbtion was not performed to increase specificity of each antiserum. This process, involving adding to the serum antigenic material of the unwanted reactant to precipitate its antibodies (Downe and Morrison, 1957) reduces antibody titre strength considerably.

Controls testing individual antisera and antigens with 0.9% saline solution showed uniformly negative results, indicating no contamination of the saline solution used in the tests. Control corixids with apparently empty guts generally also showed negative results, although some showed cross-reactions with antisera indicating the presence of some food materials in the gut. No antisera reacted with corixids themselves, as was indicated by negative results for starved animals.

Control corixids starved for short periods of time did not always produce clear negative reactions, however. Corixids were fed specific foodstuffs, then starved for periods of 0 to 90 h before testing with a range of antisera. In adults feeds were readily detectable two hours after feeding but after 20 h precipitin bands were absent or weak, and often not specific to the relevant antiserum. Starvation of the younger instars for 24 h or more produced uniformly negative serological results, perhaps related to their smaller size. Pickavance (1970) similarly found that a size difference in planarians affected

the time in which gut contents remained identifiable.

The length of time in which guts are cleared is not well known for corixids. In related hemipterans such as gerrids, which are also known to feed very occasionally on vegetable matter (Riley, 1918) guts are cleared in four to eight hours at room temperatures (Jamieson, personal communication) , but with corixids with some particulate matter in the guts this may take rather longer. Leeches and planarians may hold food in the gut for weeks, although the food substance is serologically identifiable for up to five days only, before denaturation of the proteins (Davies, 1969). It is safe to assume for corixids that foods eaten more than 24 hours prior to testing would produce weak or no serological reactions, especially in the smaller instars.

(ii) Strength of the antisera

Antiseral strength was tested in corixids recently fed specific foods; since for field collected forms there is a lack of knowledge of how long prior to capture they had ingested foods, and in what quantity.

Titre checks were run on most of the antisera to estimate their strength. Results were unsatisfactory using the method of Proom (1943), suggested also by Pickavance (1970), in which antisera diluted with 0.9% saline were tested by adding the relevant antigen to each dilution and to a control tube

containing 0.9% saline alone, and then incubating and examining for signs of precipitation.

Precipitates were obscured by cloudiness in most samples, apparently as a result of the haemolysis of the blccd during collection, resulting in dark precipitates or sediments in the serum tubes. These did not affect the Ouchterlony tests, since plasma was deposited around the point where each funnel met the agar gel (figures 18 and 19), but it rendered the methcd of Proom unworkable.

Titre strength was therefore tested by using the regular Ouchterlony plates. Dilution levels of antiserum ranged from full strength through 1:50, 1:100, 1:200, 1:400, 1:8C0, 1:1600 and 1:3200 and a control funnel containing only 0.9% saline. Results from this test indicated a minimum titre strength of 1:50 for chaoborid, daphniid and diaptomid antisera; of 1:400 for ephemeropteran, amphipod, chironomid and zygcpteran antisera, and no reactions, even at full strength, for higher plant antiserum. Reactions were seen at full strength cnly with filamentous green alga antiserum, while no blue-green alga serum was available for testing.

Pickavance (1970) suggested that a 'satisfactory' level of titre strength for his antisera was a response with a dilution of 1:8000, while Young et al. (1964) recorded a dilution sensitivity of 1:512 at best. These are higher than the present levels, even allowing for lower sensitivity of the Ouchterlony double-diffusion method than in Proom's tube method (Davies, 1969). However, Pickavance's level pertains to Planaria, which

feed infrequently, and an acceptable level for corixids need not be nearly as high, due to their different feeding habits. Indeed, since whole guts are examined, reaction with an antiserum dilution of 1:50 would ensure the recording of foods representing as little as 2% of the gut contents.

In tests the weaker antisera would be expected to produce generally weaker precipitin bands than the others for an equivalent meal size, and not to record those foods in smallest quantities. Since corixids feed frequently and are capable of feeding on a diverse collection of organisms (chapter IV), some foods might be detected in smaller amounts than others. Against this must be set the problems of different sizes of each food organisms, depending somewhat upon their instars.

So many unknowns arise here that it is safest to ignore differences in band strength when quantifying diets. In an organism feeding frequently, as do corixids, the dietary turnover is greater than in something like a planarian; therefore it is not as crucial to be able to recognise traces of previous meals.

One further point remains, the number of food items that can be detected in one gut by the test method. No empirical tests were run using double or triple feedings of specific foods, but several tests used a mixture of diaptomids and daphniids crushed and tested against the range of antisera as in a gut contents test, and these reacted with their respective antisera, producing two bands in each test. Since nearly all tests using animals fed a single foodstuff produced a single

reaction band (see section above on specificity of antisera), it can be inferred that the method is capable of revealing several foods simultaneously. It is thus superior tc the Oakley-Fulthorpe method. Figures 18 and 19 indicate the number and range of reactions seen in actual tests of field-collected corixids; reactions of adjacent antisera are separable from each other by the angle of the band to the radius, even when band ends are confluent.

RESULTS

The general corixid food pattern for certain lakes in central British Columbia was determined by serological analysis of gut contents of 1879 corixids of six species, listed in Table XXVII. These guts were tested with 11 antisera, one of which (aquatic macrophytes) proved to be non-reactive. In all corixid species less than one percent of antiserum reactions were positive for blue-green algae and snails, and mcst analyses showed a positive reaction with chironomid and zygopteran antisera, indicating a pronounced carnivorcus habit fcr these Corixidae (Table XXVIII).

Despite major similarities between the overall feeding patterns of each species, differences in the food spectrum were seen in these analyses. This is to be expected since corixid species in the more freshwater lakes studied would encounter

Table XXVII. Summary of serological data for six corixid species. Number of times each antiserum was tested with each species.

CORIXID :	Ceno-corixa bifida	Ceno-corixa expleta	Hespero-corixa laevigata	Calli-corixa audeni	Cymatia ameri--cana	Sigara species
ANTISERUM :						
Diaptomid	1232	565	38	23	10	11
Daphniid	1109	509	33	17	10	11
Amphipod	1232	565	38	23	10	11
Chaoborid	1232	565	38	23	10	11
Chironomid	1215	565	37	23	10	11
Ephemeropt	1218	565	38	23	10	11
Zygopteran	1215	565	38	23	10	11
Pulmonatan	421	168	15	22	0	11
Blue-green	803	394	17	1	3	0
Cladophora	17	0	0	0	0	0
Macrophyte	102	33	11	6	7	0
TOTALS TESTED	1232	565	38	23	10	11

Table XXVIII. Summary of serological data for six corixid species. Percentage of positive reactions to each antiserum in tests.

CORIXID :	Ceno-corixa bifida	Ceno-corixa expleta	Hespero-corixa laevigata	Calli corixa audeni	Cymatia ameri-cana	Sigara species
ANTISERUM :						
Diaptomid	14.9	22.8	5.3	0.0	10.0	9.1
Daphniid	28.3	28.5	3.0	0.0	20.0	9.1
Amphipod	4.1	0.0	2.6	8.7	10.0	0.0
Chaoborid	2.4	1.4	18.4	0.0	0.0	0.0
Chironomid	75.4	69.6	86.5	73.9	80.0	81.8
Ephemeropt	23.7	21.1	21.1	26.1	0.0	0.0
Zygopteran	56.6	55.9	63.2	60.9	60.0	63.6
Pulmonatan	0.7	0.6	0.0	0.0	0.0	0.0
Blue-green	0.6	0.0	0.0	0.0	0.0	0.0
Cladophora	17.7	0.0	0.0	0.0	0.0	0.0
Macrophyte	1.0	0.0	0.0	0.0	0.0	0.0
TOTALS TESTED	1232	565	38	23	10	11

such potential food items as amphipods and chaobcrids in abundance, organisms which are absent from or very scarce in the higher salinity lakes. Conversely, corixids in saline lakes would be exposed in nature to such forms as diaptomid copepods or fairy shrimps, which do not occur in the lower salinity water bodies (Chapter II).

Allopatric and sympatric populations of C. bifida and C. expleta may be feeding rather differently in nature, due at least partly to this difference in occurrence of many food-organisms, and perhaps also to some interspecific interaction process. Thus, since food taken may differ between instars, seasons and lakes; instar, season and lake data must be considered separately for each species. Results for the two major species of corixids, C. bifida and C. expleta , are considered first and in most detail, since most data are available for these.

Feeding pattern of C. bifida

Tables XXIX to XXXV list the feeding data, from serological analysis, for each instar of C. bifida , broken down by lake groups and seasons. As would be expected from a knowledge of the life cycle of these insects, first instars were commonest in May and June collections (season 1), and third to fifth instars were abundant in midsummer. Almost no young instars were available for collection in fall (Chapter III), limiting the seasonal

comparisons that can be made.

In 108 first instar nymphs tested (table XXIX) only zygopterans were recorded significantly (at the 5% level) more often in guts of corixids collected in the more freshwater lakes than in those from the more alkaline lakes (p=0.03). Out of 205 second instar nymphs examined (table XXX) this zygopteran food pattern was again seen, but as a non-significant trend (p=0.10). Significantly more positive precipitin results were recorded with daphniid antiserum (p=0.02) in first and second instar larvae from the more alkaline lakes compared with the freshwater lakes. No positive reactions were recorded for amphipods or chaoborids in first and second instar corixids from the more alkaline lakes, where these potential food items do not occur regularly. In both lake groups, ephemeropterans were more frequently recorded in the diet of first and second instars in summer than in spring (p=0.02 for the more alkaline lakes; p=0.07 for the more freshwater lakes).

In the guts of 224 third instar C. bifida tested (table XXXI), the number of positive reactions to daphniids differed between lakes in both spring (p=0.01) and summer (p=0.02); in both seasons daphniids were recorded significantly more frequently in guts from higher salinity lakes. A similar though statistically non-significant trend was seen for diaptomids (p=0.06) in summer samples. More third instar guts contained ephemeropterans in summer than in spring samples in both lake groups (p=0.00 for the more alkaline lake, but results were non-significant for the more freshwater bodies).

Table XXIX. Feeding pattern of first instar C. bifida arranged by lakes and seasons.
Data expressed as percentages feeding on each foodstuff, and totals examined, for each lake and season.

Serum	lake 2 spring	lake 2 summer	lake 2 fall	lake 3 spring	lake 3 summer	lake 3 fall	totals
Diapt	0.0 29	16.7 6		0.0 72	0.0 1		0.9 108
Daph	3.5 29	0.0 4		2.8 72	0.0 1		2.8 106
Amphi	0.0 29	0.0 6		0.0 72	0.0 1		0.0 108
Chaob	0.0 29	0.0 6		0.0 72	0.0 1		0.0 108
Chiro	34.5 29	16.7 6		50.0 72	100.0 1		44.4 108
Eph	0.0 29	16.7 6		1.4 72	100.0 1		2.8 108
Zyg	3.5 29	16.7 6		30.6 72	100.0 1		23.1 108
Pulm		0.0 6		0.0 12	0.0 1		0.0 19
Blue-g	0.0 29			0.0 60			0.0 89
Macro		0.0 2					0.0 2

Table XXX. Feeding habits of second instar _C_. _bifida_ arranged by lakes and seasons.
Data expressed as percentages feeding on each foodstuff, and totals examined, for each lake and season.

Serum	lake 2 spring	lake 2 summer	lake 2 fall	lake 3 spring	lake 3 summer	lake 3 fall	totals
Diapt	1.4 73	9.1 22		6.5 92	0.0 18		4.4 205
Daph	13.7 73	11.1 9		2.2 92	0.0 18		6.8 192
Amphi	0.0 73	0.0 22		2.2 92	0.0 18		1.0 205
Chaob	0.0 73	4.6 22		12.0 92	5.6 18		6.3 205
Chiro	69.9 73	90.9 22		77.2 92	100.0 18		78.0 205
Eph	1.4 73	18.2 22		3.3 92	27.8 18		6.3 205
Zyg	31.5 73	54.5 22		53.3 92	66.7 18		46.8 205
Pulm	0.0 20	0.0 21		4.2 24	0.0 18		1.2 83
Blue-g	1.9 53	0.0 1		0.0 69			0.8 123
Macro		0.0 13					0.0 13

Table XXXI. Feeding pattern of third instar of C. bifida arranged by lakes and seasons
Data expressed as percentages feeding on each foodstuff, and totals examined, for each lake and season.

Serum	lake 2 spring	lake 2 summer	lake 2 fall	lake 3 spring	lake 3 summer	lake 3 fall	tctals
Diapt	16.4 61	27.7 101	0.0 1	4.7 43	0.0 18		17.9 224
Daph	49.2 61	40.7 91	0.0 1	14.0 43	0.0 18		34.1 214
Amphi	0.0 61	0.0 101	0.0 1	2.3 43	5.6 18		0.9 224
Chaob	3.3 61	2.0 101	0.0 1	2.3 43	11.1 18		3.1 224
Chiro	82.0 61	84.2 101	100. 1	88.4 43	77.8 18		83.9 224
Eph	16.4 61	56.4 101	0.0 1	9.3 43	22.2 18		33.5 224
Zyg	50.8 61	76.2 101	100. 1	79.1 43	44.4 18		67.4 224
Pulm	0.0 12	2.3 43		0.0 10	0.0 18		1.2 83
Blue-g	0.0 49	1.8 57	0.0 1	0.0 33			0.7 140
Macro		0.0 3					0.0 3

Table XXXII indicates that for 217 fourth instars examined, there were again more positive reactions to daphniids (p=0.01) and diaptomids (p=0.06) in summer samples collected in higher alkalinity lakes than in the lower alkaline lake group (lake group 3). Ephemeropterans were again more frequently recorded in fourth instar guts collected in the summer in alkaline lakes than in spring (p=0.01). A similar result was found with diaptomids (p=0.08), but the opposite situation was observed for daphniids (p=0.01).

In alkaline lake samples occasional reactions were recorded with chaoborid and amphipod antiserum; however, these organisms have only occasionally been recorded in Round-up Lake (see Chapter II), and thus may not in fact be available in the normal environment as food. These positive reactions may alternatively represent a spreading of specificity from related crustaceans following the use of an adjuvant in antiserum preparation. Occasionally, a similar reaction occurred with diaptomid antiserum in guts collected in the more freshwater lakes, where diaptomids do not occur (chapter II).

Table XXXIII lists data for 96 fifth instar nymphs of C. bifida , most of which were collected in the higher salinity lakes. Gut content reaction patterns were generally similar between lakes and seasons. Again, occasional records for positive reactions to amphipods and chaoborids occurred with insects taken from the higher salinity lakes.

Most of the 175 adult female C. bifida examined were

Table XXXII. Feeding pattern of fourth instar of C. bifida arranged by lakes and seasons.
Data expressed as pecentages feeding on each foodstuff, and totals examined, for each lake and season.

Serum	lake 2 spring	lake 2 summer	lake 2 fall	lake 3 spring	lake 3 summer	lake 3 fall	totals
Diapt	10.9 46	28.3 113	50.0 2	0.0 1	10.9 55		20.3 217
Daph	69.6 46	31.8 107	50.0 1	100.0 1	2.9 34		36.5 189
Amphi	0.0 46	0.9 113	0.0 2	0.0 1	9.1 55		2.8 217
Chaob	4.3 46	1.8 113	0.0 2	0.0 1	1.8 55		2.3 217
Chiro	80.4 46	77.9 113	50.0 2	100.0 1	92.7 55		82.0 217
Eph	8.7 46	39.8 113	0.0.2	0.0 1	30.9 55		28.6 217
Zyg	54.3 46	68.1 113	50.0 2	0.0 1	70.9 55		65.4 217
Pulm	0.0 19	0.0 43		0.0 1	0.0 55		0.0 118
Blue-g	0.0 27	0.0 70	0.0 2				0.0 99
Macro		0.0 1			0.0 21		0.0 22

Table XXXII. Feeding pattern of fourth instar of $\underline{C}$. $\underline{bifida}$ arranged by lakes and seasons.
Data expressed as pecentages feeding cn each fccdstuff, and totals examined, for each lake and season.

Serum	lake 2 spring	lake 2 summer	lake 2 fall	lake 3 spring	lake 3 summer	lake 3 fall	totals
Diapt	10.9 46	28.3 113	50.0 2	0.0 1	10.9 55		20.3 217
Daph	69.6 46	31.8 107	50.0 1	100.0 1	2.9 34		36.5 189
Amphi	0.0 46	0.9 113	0.0 2	0.0 1	9.1 55		2.8 217
Chaob	4.3 46	1.8 113	0.0 2	0.0 1	1.8 55		2.3 217
Chiro	80.4 46	77.9 113	50.0 2	100.0 1	92.7 55		82.0 217
Eph	8.7 46	39.8 113	0.0.2	0.0 1	30.9 55		28.6 217
Zyg	54.3 46	68.1 113	50.0 2	0.0 1	70.9 55		65.4 217
Pulm	0.0 19	0.0 43		0.0 1	0.0 55		0.0 118
Blue-g	0.0 27	0.0 70	0.0 2				0.0 99
Macro		0.0 1			0.0 21		0.0 22

Table XXXIII. Feeding pattern of fifth instar C. bifida
arranged by lakes and seasons
Data expressed as percentages feeding on each foodstuff, and totals
examined, for each lake and season.

Serum	lake 2 spring	lake 2 summer	lake 2 fall	lake 3 spring	lake 3 summer	lake 3 fall	totals
Diapt	100.0 1	35.1 77	20.0 10		33.3 6	0.0 2	33.3 96
Daph	100.0 1	51.6 64	33.3 9		16.7 6		47.5 80
Amphi	0.0 1	1.3 77	0.0 10		66.7 6	0.0 2	5.2 96
Chaob	0.0 1	1.3 77	0.0 10		0.0 6	0.0 2	1.0 96
Chiro	0.0 1	72.7 77	70.0 10		66.7 6	100.0 2	71.9 96
Eph	100.0 1	61.0 77	20.0 10		66.7 6	50.0 2	57.3 96
Zyg	100.0 1	58.4 77	80.0 10		83.3 6	50.0 2	62.5 96
Pulm		3.4 29			0.0 4	0.0 2	2.9 35
Blue-g	0.0 1	2.1 48	0.0 10		0.0 2		1.6 61
Macro		0.0 7				0.0 2	0.0 9

collected in the higher alkalinity lakes (Table XXXIV). There was a non-significant trend for more positive records for daphniids in guts from spring-collected insects from higher alkaline lakes than in those from the fresher water bodies (p=0.1). Of guts from the higher alkalinity lake insects tested with ephemeropteran antiserum, significantly more positive reactions were recorded in summer than in fall (p=0.01) and in summer than in spring (p=0.07), However in the case of amphipods, more reactions were seen in spring (p=0.06) and summer (p=0.01) than in fall samples from freshwaters.

In the 205 males of C. bifida tested (table XXXV) several similar trends were seen. Ephemeropterans were again significantly most often recorded in guts of insects collected in the more alkaline lakes in summer than in fall (p=0.01) or spring (p=0.01), and amphipods were detected more frequently in spring (p=0.1) and summer (p=0.01) than in fall in the more freshwater lakes.

In adult males and females, as in the juvenile instars, occasional reactions were recorded with diaptomids, amphipods and chaoborids in guts from lake groups where these organisms apparently do not occur. These reactions occurred in 1.7% of guts with chaoborid antiserum and 0.5% with amphipod antiserum in the higher alkalinity lakes, and 4.7% with diaptomid antiserum in the freshwater lakes. These discrepancy rates for adults are not altered markedly when all instars are considered together.

Positive reactions were observed in 0.63% of tests with all

Table XXXIV. Feeding pattern of adult female C. bifida arranged by lakes and seasons.
Data expressed as percentages feeding on each foodstuff, and totals examined, for each lake and season.

Serum	lake 2 spring	lake 2 summer	lake 2 fall	lake 3 spring	lake 3 summer	lake 3 fall	totals
Diapt	26.1 23	15.0 20	13.1 61	6.3 32	10.0 10	0.0 29	11.4 175
Daph	47.8 23	50.0 6	38.3 60	15.6 32	20.0 10	30.8 26	33.1 157
Amphi	0.0 23	0.0 20	0.0 61	28.1 32	60.0 10	3.4 29	9.1 175
Chaob	4.3 23	0.0 20	0.0 61	3.1 32	0.0 10	0.0 29	1.1 175
Chirc	80.5 21	65.0 20	68.9 61	74.1 27	90.0 10	62.1 29	68.8 173
Eph	9.5 21	50.0 20	9.8 61	14.8 27	20.0 10	20.7 29	17.9 168
Zyg	47.6 21	50.0 20	54.1 61	48.1 27	60.0 10	51.7 29	53.0 168
Pulm		0.0 15	0.0 2		0.0 2	0.0 10	0.0 29
Blue-g	0.0 23	0.0 5	1.7 59	0.0 32	0.0 8	0.0 15	0.7 142
Macro		0.0 14				0.0 6	0.0 20
Green	0.0 2			20.0 5			14.3 7

Table XXXV. Feeding pattern of adult male C. bifida arranged by lakes and seasons
Data expressed as percentages feeding on each foodstuff, and totals examined for each lake and season.

Serum	lake 2 spring	lake 2 summer	lake 2 fall	lake 3 spring	lake 3 summer	lake 3 fall	totals
Diapt	21.7 23	34.3 35	25.8 62	0.0 24	4.8 21	5.0 40	17.6 205
Daph	47.8 23	25.0 8	37.9 66	41.6 24	23.8 21	35.1 37	36.9 179
Amphi	8.7 23	0.0 35	0.0 62	25.0 24	42.9 21	5.0 40	9.3 205
Chaob	4.3 23	2.9 35	0.0 62	0.0 24	0.0 21	0.0 40	1.0 205
Chirc	81.3 16	85.7 35	66.1 62	90.5 21	90.5 21	75.0 40	77.9 195
Eph	5.3 19	60.0 35	19.4 62	4.2 21	23.8 21	15.0 40	23.2 198
Zyg	62.5 16	65.7 35	67.7 62	57.1 21	66.7 21	62.5 40	64.6 195
Pulm	0.0 3	0.0 31	0.0 3		0.0 9	0.0 8	0.0 54
Blue-g	4.3 23	0.0 4	0.0 57	0.0 24	0.0 12	0.0 27	0.7 147
Macro		4.0 25	0.0 2			0.0 6	3.0 33
Green	14.7 7			50.0 2			22.2 9

instars with blue-green algae antiserum and in 0.71% with pulmonate antiserum. This low level of reactions suggests a definite lack of feeding on these items. Results with the aquatic macrophyte antiserum were at a similar level of 0.98%, (one positive reaction in 102 tests). This last antiserum gave no positive reactions in initial tests of antisera.

Feeding pattern of C. expleta

Tables XXXVI to XLII contain the serological results for all C. expleta tested, with instar, season and lake data considered separately. There were no spring samples collected in the highest salinity water (Lake LB 2), and, as expected, fall samples did not contain any of the youngest instars.

In the 17 first instar nymphs tested (table XXXVI), no significant pattern of variation in numbers of positive reactions to different antisera was discernable. Of 73 second instar C. expleta (table XXXVII) the only marked trend seen was in the numbers of positive reactions to daphniids; these were greater in spring than in summer samples (p=0.08) from the Becher's Prairie lakes of group 2.

A similar trend was seen among the 116 third instar nymphs (table XXXVIII) where more positive reactions were recorded in these lakes in spring (p=0.01 and in fall (p=0.11) than in summer. In contrast, fewer positive reactions were noted for ephemeropterans in spring than in either summer (p=0.04) or fall

Table XXXVI. Feeding pattern of first instar C. expleta arranged by lakes and seasons
Data expressed as percentages feeding on each foodstuff, and totals examined, for each lake and season.

Serum	lake 1 spring	lake 1 summer	lake 1 fall	lake 2 spring	lake 2 summer	lake 2 fall	totals
Diapt		0.0 10			0.0 7		0.0 17
Daph		20.0 10			0.0 7		11.8 17
Amphi		0.0 10			0.0 7		0.0 17
Chaob		0.0 10			0.0 7		0.0 17
Chiro		90.0 10			57.1 7		76.5 17
Eph		10.0 10			0.0 7		5.9 17
Zyg		50.0 10			14.3 7		35.3 17
Pulm					0.0 7		0.0 7
Blue-g		0.0 10					0.0 10

Table XXXVII. Feeding pattern of second instar C. expleta arranged by lakes and seasons.
Data expressed as percentages feeding on each foodstuff, and totals examined, for each lake and season.

Serum	lake 1 spring	lake 1 summer	lake 1 fall	lake 2 spring	lake 2 summer	lake 2 fall	totals
Diapt		23.8 21		0.0 11	16.0 25	31.3 16	19.2 73
Daph		33.3 21		54.5 11	0.0 11	31.3 16	30.5 59
Amphi		0.0 21		0.0 11	0.0 25	0.0 16	0.0 73
Chaob		0.0 21		0.0 11	4.0 25	0.0 16	1.4 73
Chirc		85.7 21		72.7 11	64.0 25	93.8 16	78.1 73
Eph		4.8 21		9.1 11	24.0 25	37.5 16	19.2 73
Zyg		71.4 21		27.3 11	68.0 25	75.0 16	64.4 73
Pulm				0.0 5	0.0 25	0.0 2	0.0 32
Blue-g		0.0 21		0.0 6		0.0 14	0.0 41
Macro					0.0 13		0.0 13

Table XXXVIII. Feeding pattern of third instar C. expleta arranged by lakes and seasons.
Data expressed as percentages feeding on each foodstuff, and totals examined, for each lake and season.

Serum	lake 1 spring	lake 1 summer	lake 1 fall	lake 2 spring	lake 2 summer	lake 2 fall	totals
Diapt		14.3 42	0.0 2	4.8 21	14.3 35	31.3 16	14.7 116
Daph		31.0 42	50.0 2	95.2 21	7.7 13	56.3 16	46.8 94
Amphi		0.0 42	0.0 2	0.0 21	0.0 35	0.0 16	0.0 116
Chaob		7.1 42	0.0 2	4.8 21	2.9 35	6.3 16	5.2 116
Chiro		90.5 42	50.0 2	47.6 21	62.9 35	87.5 16	73.3 116
Eph		9.1 44	0.0 2	4.8 21	42.9 35	43.8 16	22.9 118
Zyg		76.2 42	50.0 2	66.7 21	71.4 35	75.0 16	72.4 116
Pulm				0.0 9	0.0 33	0.0 2	0.0 44
Blue-g		0.0 42	0.0 2	0.0 12	0.0 2	0.0 13	0.0 71
Macro					0.0 10	0.0 1	0.0 11

(p=0.06) samples. In the third instar summer samples, significantly more guts showed a positive reaction for ephemeropterans in the Becher's Prairie lakes than in Lake LB 2. However, since the faunal components of Lake LB 2 were not investigated in detail, the full significance of this difference is not clear.

In the 81 fourth instar C. expleta tested (table XXXIX) differences significant at the 5% level were only detected in the Becher's Prairie lakes. Here, more positive reactions to daphniids were recorded in spring than in summer guts (p=0.00) but there were more positive reactions to ephemeropterans in summer than in spring (p=0.05). All other differences noted were not statistically significant.

Table XL lists the results for the 54 fifth instar nymphs of C. expleta examined. As is to be expected, no fifth instar insects were taken in the spring season in either lake group; numbers were greatest in fall collections.

The fifth instar C. expleta results are rather different from those in fifth instar C. bifida , and this is related to the presence of a late third generation in C. expleta in LB 2 and the highest salinity Becher's Prairie lakes, thus introducing a seasonal effect in feeding of similar instars in the two species. Numbers of C. expleta were only large enough to compare fall collections between the two lake groups. In these, significantly more positive reactions to daphniids and ephemeropterans were recorded in guts from the Becher's Prairie lakes than in those from Lake LB 2, although with other antisera

Table XXXIX. Feeding Pattern of fourth instar C. expleta arranged by lakes and seasons.
Data expressed as percentages feeding on each foodstuff, and totals examined, for each lake and season.

Serum	lake 1 spring	lake 1 summer	lake 1 fall	lake 2 spring	lake 2 summer	lake 2 fall	totals
Diapt		50.0 4	28.6 21	8.7 23	11.1 27	33.3 6	18.5 81
Daph		25.0 4	14.3 21	91.3 23	0.0 18	20.0 5	36.6 71
Amphi		0.0 4	0.0 21	0.0 23	0.0 27	0.0 6	0.0 81
Chaob		0.0 4	0.0 21	0.0 23	0.0 27	16.7 6	1.2 81
Chiro		0.0 4	85.7 21	69.6 23	63.0 27	83.3 6	69.1 81
Eph		25.0 4	19.0 21	0.0 23	25.9 27	33.3 6	17.3 81
Zyg		100.0 4	81.0 21	43.5 23	59.3 27	66.7 6	63.0 81
Pulm				0.0 2	3.8 26	0.0 3	3.2 31
Blue-g		0.0 4	0.0 21	0.0 21	0.0 1	0.0 3	0.0 50
Macro					0.0 3		0.0 3

Table XL. Feeding pattern of fifth instar $\underline{C}$. $\underline{expleta}$ arranged by lakes and seasons.
Data expressed as percentages feeding on each foodstuff, and totals examined, for each lake and season.

Serum	lake 1 spring	lake 1 summer	lake 1 fall	lake 2 spring	lake 2 summer	lake 2 fall	totals
Diapt		33.3 3	32.8 64		0.0 4	24.1 54	28.0 125
Daph		0.0 3	14.1 64		0.0 3	40.7 54	25.0 124
Amphi		0.0 3	0.0 64		0.0 4	0.0 54	0.0 125
Chaob		0.0 3	0.0 64		0.0 4	0.0 54	0.0 125
Chiro		33.3 3	62.5 64		50.0 4	68.5 54	64.0 125
Eph		33.3 3	14.1 64		50.0 4	40.7 54	27.2 124
Zyg		33.3 3	51.6 64		50.0 4	68.5 54	58.4 125
Pulm		0.0 3			0.0 4	0.0 2	0.0 9
Blue-g			0.0 64			0.0 51	0.0 115
Macro						0.0 1	0.0 1

no differences were observed.

Results for 61 female C. expleta examined are given in Table XLI. Seasonal differences were seen in the high salinity lake group 1 (LB 2) for numbers of positive reactions for diaptomids (p=0.01); these were only recorded in fall. There was also a similar but non-significant trend in this lake for daphniids (p=0.14).

Table XLII lists results for 81 male C. expleta , chiefly collected in the high salinity lake LB 2. The distribution of samples precluded statistical comparisons of data between lake groups. However, in Lake LB 2 there was a trend (non-significant) for the number of guts reacting with ephemeropteran antiserum to be greater in summer than in fall (p=0.08). The reverse was seen for diaptomids (p=0.02).

In C. expleta guts, as in C. bifida , some reactions were seen for organisms that had not been recorded from the collection sites. Although no reactions were seen in 844 tests with amphipod antiserum, 1.4% of guts tested reacted positively with chaoborid antiserum in lake groups 1 and 2. Guts reacting positively were only found in second to fourth instar insects. Chaoborids may have been present in Round-up Lake on Becher's Prairie (chapter II). No positive reactions were recorded with aquatic macrophyte or blue-green algal antisera; since the former was inert in tests of specificity and strength, it may be considered a control solution. One out of 157 tests of C. expleta guts with pulmonate antiserums showed positive for the higher salinity lakes in Becher's Prairie ; this is likely

Table XLI. Feeding pattern of female adult C. expleta arranged by lakes and seasons
#data expressed as percentages feeding on each foodstuff and totals examined, for each lake and season.

Serum	lake 1 spring	lake 1 summer	lake 1 fall	lake 2 spring	lake 2 summer	lake 2 fall	totals
Diapt		0.0 20	46.9 32	0.0 1	0.0 1	0.0 7	24.6 61
Daph		0.0 20	19.4 31	0.0 1		57.1 7	16.9 59
Amphi		0.0 20	0.0 32	0.0 1	0.0 1	0.0 7	0.0 61
Chaob		0.0 20	0.0 32	0.0 1	0.0 1	0.0 7	0.0 61
Chiro		45.0 20	59.4 32	0.0 1	0.0 1	57.1 7	52.5 61
Eph		5.0 20	19.4 32	0.0 1	0.0 1	0.0 7	11.5 61
Zyg		15.0 20	43.8 32	0.0 1	0.0 1	71.4 7	36.1 61
Pulm		0.0 19	0.0 1		0.0 1		0.0 21
Blue-g		0.0 1	0.0 31	0.0 1		0.0 6	0.0 39
Macro			0.0 1		0.0 1	0.0 1	0.0 3

Table XIII. Feeding pattern of adult male C. expleta arranged
by lakes and seasons
#data expressed as percentages feeding on each fccstuff and totals
examined, for each lake and season.

Serum	lake 1 spring	lake 1 summer	lake 1 fall	lake 2 spring	lake 2 summer	lake 2 fall	totals
Diapt		5.6 18	52.6 57			33.3 6	40.7 81
Daph		5.6 18	14.5 55			1CC.0 4	16.9 77
Amphi		0.0 18	0.0 57			0.0 6	0.0 81
Chaob		0.0 18	0.0 57			0.0 6	0.0 81
Chirc		72.2 18	68.4 57			83.3 6	70.4 81
Eph		50.0 18	17.5 57			50.0 6	27.2 81
Zyg		44.4 18	35.1 57			33.3 6	37.0 81
Pulm		0.0 18	0.0 2				0.0 20
Blue-g			0.0 55			C.0 6	0.0 61
Macro			0.0 2				0.0 2

to be an experimental or reading error, as it is at a similar
level to that recorded for pulmonates in C. bifida , and as
pulmonates were not recorded from the higher salinity lakes.

Differences in feeding pattern of Cenocorixa males and females

For every serum tested against gut contents of field-
collected adult Cenocorixa , males showed as many as or more
positive reactions than females, although in many cases the
trend was not marked (tables XLIII, XLIV). Little or no
difference between the sexes was seen in numbers recorded
feeding on chaoborids, amphipods, filamentous green algae and
aquatic macrophytes for C. bifida , and on daphniids and
zygopterans for C. expleta .

Significantly greater proportions of positive reactions in
males of C. expleta were recorded for ephemeropteran antiserum,
and in C. bifida males with zygopteran antiserum. Other marked
trends were seen for both species with diaptomids and
chironomids. None of these trends were affected by seasonal
differences in proportions of positive reactions. Thus in the
analysis of the results there is some level of feeding bias
introduced by pooling feeding data for both sexes of adult.

In the analysis of serological results, no information was
recorded on the relative feeding levels of tenerals and old
adults. Feeding experiments (chapter IV), however, indicate that
tenerals may feed at a higher level, and so pooling results may

Table XLIII. Differences in feeding pattern of male and female
<u>C</u>. <u>bifida</u> and <u>C</u>. <u>expleta</u> , expressed as percentages reacting
positively with each antiserum.

| | <u>C</u>. <u>bifida</u> | | | | <u>C</u>. <u>expleta</u> | | | |
| | females | | males | | females | | males | |
ANTISERUM	n=	(%)	n=	(%)	n=	(%)	n=	(%)
Diaptomids	176	11.9	206	17.5	61	24.6	81	40.7
Daphniids	158	32.9	170	38.8	59	18.6	77	16.9
Amphipods	176	9.1	206	9.2	61	0.0	81	0.0
Chaoborids	176	1.1	206	1.0	61	0.0	81	0.0
Chironomids	169	71.0	196	78.1	61	54.1	81	70.4
Ephemeropt.	169	17.8	199	23.1	61	11.5	81	37.3
Zygopterans	169	51.5	196	64.8	61	37.7	81	38.8
Pulmonates	29	0.0	54	0.0	21	0.0	20	0.0
Blue-greens	143	0.7	148	0.7	39	0.0	61	0.0
Cladophora	7	14.3	10	20.0				
Macrophytes	20	0.0	33	3.0	3	0.0	2	0.0
ALL FOODS	1392	23.7	1624	27.9	488	18.2	646	24.0

Table XLIV. Differences in feeding pattern of male and female C. bifida and C. expleta . Probabilities from chi square data.

FOOD ITEM	C. bifida SUPERIOR SEX	P=	C. expleta SUPERIOR SEX	P=
Diaptomids	MALE	0.17	MALE	0.06
Daphniids	MALE	0.32	MALE	0.92
Amphipods	MALE	0.86		
Chaoborids	MALE	0.73		
Chironomids	MALE	0.15	MALE	0.07
Ephemeropt.	MALE	0.25	MALE	0.04
Zygopterans	MALE	0.01	MALE	0.89
Cladophora	MALE	0.73		
Macrophytes	MALE	0.79		
ALL FOODS	MALE	0.01	MALE	0.02

mask a bias of undetermined proportions here.

Feeding patterns of Cenocorixa from different lakes

Results here are considered for different lake groups, but pooled for seasons of collection. In the next section results are pooled by lakes but contrasted by season. This has been done to determine how results might be biassed by pooling data of diverse spatial and temporal origin, since the realised niches in each environment may differ.

First, considering adults, differences between lakes are significant only for daphniids in the diet of adult C. expleta in the Becher's Prairie and LB 2 localities (p=0.00), reflecting probably the sparseness of daphniids in the latter lake. Marked though not statistically significant trends with this food were also seen for C. bifida (p=0.09), the positive serological reactions being fewer in freshwater lakes than in the moderately saline lakes . A similar trend in adult C. bifida was seen with ephemeropterans; more positive reactions being recorded in the moderately saline lakes (p=0.19). Both these results may reflect the generally greater variety of food items available in the more freshwater lakes (chapter II): thus, individual food items might figure less frequently in the diet when there is a greater variety of food.

More adult C. expleta were recorded as having fed on diaptomids in Lake LB 2 than in the Becher's Prairie lakes

(p=0.29), this food in LB 2 perhaps taking the place of daphniids in the diet. Results with chironomid and zygopteran antisera showed no significant trends between the different lake groups.

When instars of each species are examined separately, and all significant or near-significant (p<0.1) differences in positive reactions to foods assessed, reactions to zygopterans were consistently most frequent in the most freshwater lakes, and to daphniids and ephemeropterans in the moderately high saline lakes.

The pooled data for all instars of C. expleta indicate significant difference between lake groups in numbers reacting with diaptomid (p=0.00), ephemeropteran (p=0.00) and zygopteran (p=0.02) antisera, in contrast to the results with adults alone. However, reactions with daphniid antiserum remain at a significantly different level (p=0.00) when either adults alone, or all instars together, are considered. This would seem to indicate that the juveniles may depend more strongly on diaptomids, ephemeropterans and zygopterans than do the adults, although both juveniles and adults feed at fairly similar levels on daphniids.

The pooled data for all instars of C. bifida show significantly more positive reactions for daphniids and ephemeropterans in the moderately saline lakes than in freshwater lakes (p=0.00 for each), again indicating different dietary emphasis by different larval instars: adults when considered alone did not show these differences.

Thus if instars are treated separately, significant bias will not be introduced into the results through pooling all data from different lakes, except where some food items are restricted to a few lakes.

Feeding patterns of _Cenocorixa_ collected at different seasons

In most cases, analysis of pooled data indicated no significant differences in positive reactions for foodstuffs in guts of insects collected at different times of year. However, the numbers of positive reactions for diaptomids were significantly greater in fall than in summer for _C. expleta_ collected from Lake LB 2 (p=0.00). By contrast, numbers of _C. bifida_ reacting positively with amphipod antiserum in the more freshwater lakes were higher in summer than in fall (p=0.00) or spring (p=0.01), and similar results were seen in the more saline lakes with ephemeropteran antiserum (p=0.00 for both seasons). The higher number of positive reactions recorded with summer-collected samples may correlate either with higher temperatures and greater feeding, and/or with a period of greater abundance of these foodstuffs at a size suitable for capture. Looking at individual instars, highest positive reaction rates for ephemeropteran and amphipod antisera were again consistently seen in summer, while evidence of feeding on daphniids was consistently most frequent in spring and fall.

Approximately equal percentages of positive precipitin

reactions in guts of C. bifida were recorded in all seasons for chironomids, zygopterans and diaptomids in all lakes studied. This indicates that bias may only be introduced when data are pooled for corixids collected at different seasons, in the case of certain foodstuffs such as amphipods and ephemeropterans. However, since over 20% of guts may show positive reactions with ephemeropteran antiserum, further analysis should discriminate between seasons of collection wherever this foodstuff is frequent. Further, since positive reactions with ephemeropteran antiserum were commonest in mid-summer, this indicates the difficulty of summarising feeding pattern by pooling data for different lakes, seasons, instars, and so on, without weighting them somehow to allow for different numbers present at different times in different lakes.

Differences between feeding patterns of Cenocorixa in sympatry

The detailed analysis of serological results presented above indicates that for certain foodstuffs there are marked and often statistically significant differences in proportions of positive reactions from lake to lake, and with season, in each species of Cenocorixa . This may be due to differences in the distribution pattern and/or abundance of the organisms. However, it may also be due to some interactive behaviour pattern between the species of Cenocorixa in sympatry. Typically, this might be expected to be reflected as lessened competition in sympatry for those foodstuffs eaten equally by both species. Therefore, the

species are next compared to look for evidence of dietary differences in sympatry.

Results of analysis of feeding pattern by instar for both species in sympatry are given in Table XLV, expressed as percentages of positive reactions in guts tested, and total numbers tested. The data indicate first that both species in general feed upon the same items of food in sympatry. The order of importance of dietary items in all instars of C. bifida was chironomids, then zygopterans, followed usually by daphniids, ephemeropterans and diaptomids. This same pattern was also seen in most juvenile instars of C. expleta . However, in the third instar of C. expleta the greatest proportion of positive reactions was seen in response to zygopteran antiserum, and in adults, most reactions were with daphniid antiserum.

Table XLV again indicates an increase in the level of positive reactions for most antisera (representing foods), with increased instar size, a feature seen first in the individual Tables XXIX to XLII. Whereas this in general reaches a plateau level in C. bifida by about the third instar, in C. expleta the plateau level of mean acceptability is often reached by the second instar. This is probably related to the size difference between the species; all instars of C. expleta being slightly larger than the corresponding stages of C. bifida , and may represent the physical limits of size, swimming speed and strength needed to capture each prey type. For instance, positive reactions to diaptomid antiserum jumped to a level of over 20% in C. bifida in the third instar, after a level of 2%

Table XLV. Feeding patterns of separate instars of C. bifida and C. expleta expressed as percentage positive reactions with each antiserum.

INSTARS: antisera	Cenocorixa species	1	2	3	4	5	ALS
Diaptomids	bifida	2.9	3.2	23.3	23.6	34.1	22.3
	expl.	0.0	17.3	15.3	12.5	22.4	13.3
Daphniids	bifida	3.0	13.4	43.8	43.5	50.0	42.6
	expl.	0.0	29.0	60.0	47.8	40.7	75.0
Amphipods	bifida	0.0	0.0	0.0	0.6	1.1	0.9
	expl.	0.0	0.0	0.0	0.0	0.0	0.0
Chaoborids	bifida	0.0	1.1	2.5	2.5	1.1	1.3
	expl.	0.0	1.9	4.2	1.8	0.0	0.0
Chironomids	bifida	31.4	74.7	83.4	78.3	71.6	72.6
	expl.	57.1	75.0	63.9	67.9	67.2	66.7
Ephemeropt.	bifida	2.9	5.3	41.1	30.4	56.8	23.9
	expl.	0.0	25.0	31.9	16.1	41.4	20.0
Zygopterans	bifida	5.7	36.8	66.4	64.0	61.4	59.5
	expl.	14.3	61.5	70.8	53.6	67.2	53.3
Pulmonates	bifida	0.0	0.0	1.8	0.0	3.5	0.0
	expl.	0.0	0.0	0.0	3.2	0.0	0.0
Blue-greens	bifida	0.0	1.9	0.9	0.0	1.7	1.2
	expl.	0.0	0.0	0.0	0.0	0.0	0.0
Macrophytes	bifida	0.0	0.0	0.0	0.0	0.0	2.4
	expl.	0.0	0.0	0.0	0.0	0.0	0.0
ALL FOODS NUMBERS TESTED	bifida	5.7 35	16.7 95	32.6 163	30.3 161	34.2 88	26.6 224
ALL FOODS NUMBERS TESTED	expl.	8.9 7	25.3 52	29.1 72	24.5 56	29.8 58	27.1 15

to 3% in smaller instars, whereas second instar C. expleta had already reached the plateau level for this species of over 15%. Size differences between equivalent instars of C. bifida and C. expleta are nevertheless not sufficiently great to make, for example, the third instar of C. bifida more comparable to second instar than third instar C. expleta .

Table XLVI shows the results of chi-square tests of significance in comparisons between the species at each instar in sympatry. There were no significant differences in the first instar, but by the second the proportions of positive reactions with diaptomid, ephemeropteran and zygopteran antisera were significantly greater in C. expleta than in C. bifida , and almost significantly so with daphniids. In the third instar significantly more guts of C. bifida showed positive reactions for chironomids than those of C. expleta , and in the fourth, there were generally greater levels of positive reactions with all foods in guts of C. bifida than of C. expleta . In neither this nor the fifth instar did C. expleta show relatively more positive reactions to any antiserum than C. bifida .

In summary, although both Cenocorixa species took the same food items in sympatry, in earliest instars C. expleta generally showed more positive reactions than C. bifida for diaptomids, daphniids and zygopterans, but in later instars this was reversed. Among adults more C. expleta took daphniids than did C. bifida , although results for other foodstuffs were very similar between the species.

Table XLVII shows the differences between Cenocorixa

Table XLVI. Differences in feeding pattern between the instars of C. bifida and C. expleta in sympatry. Data expressed as chi square probabilities, and superior species in each case.

INSTARS:	1	2	3	4	5	ADULTS
ANTISERUM						
Diaptomid	Bi:0.39	Ex:0.01	Bi:0.22	Bi:0.11	Bi:0.18	Bi:0.62
Daphniid	Bi:0.39	Ex:0.07	Ex:0.06	Ex:0.73	Bi:0.40	Ex:0.06
Amphipod				Bi:0.59	Bi:0.81	Bi:0.27
Chaoborid		Bi:0.75	Bi:0.76	Bi:0.81	Bi:0.81	Bi:0.46
Chironomid	Ex:0.39	Bi:0.85	Bi:0.00	Bi:0.16	Bi:0.00	Bi:0.83
Ephemeropt		Ex:0.00	Bi:0.16	Bi:0.05	Bi:0.09	Bi:0.93
Zygopteran	Bi:0.95	Ex:0.01	Ex:0.66	Bi:0.22	Ex:0.59	Bi:0.82
Pulmonate			Bi:0.88	Ex:0.72	Bi:0.38	
Blue-green		Bi:0.61	Bi:0.46		Bi:0.90	Bi:0.32
Macrophyte						Bi:0.03
ALL FOODS	Ex:0.55	Ex:0.00	Bi:0.14	Bi:0.02	Bi:0.13	Ex:0.94

Table XLVII. Food preferences of sympatric C. bifida and C. expleta at different seasons.

ANTISERUM	C. bifida seasons[1] and probability[2]			C. expleta seasons[1] and probability[2]		
Diaptomid	summer 0.00	spring 0.07	fall 0.02	fall 0.02	summer 0.00	spring 0.28
Daphniid	spring 0.60	fall 0.92	summer 0.66	spring 0.00	fall 0.00	summer 0.00
Chironomid	summer 0.09	spring 0.02	fall 0.44	fall 0.03	summer 0.10	spring 0.90
Ephemeropt	summer 0.00	spring 0.00	fall 0.04	fall 0.31	summer 0.00	spring 0.00
Zygopteran	fall 0.61	summer 0.00	spring 0.00	fall 0.37	summer 0.03	spring 0.21

[1]Seasons listed in order of greatest percentage feeding.
[2]Column 1: probability between first and second season listed
  Column 2: probability between first and last season
  Column 3: probability between second and last season

species at different seasons in sympatry. C. bifida showed most positive reactions to diaptomid, chironomid and ephemeropteran antisera in summer and least in fall, although reactions with zygopteran antiserum were at a high level in both summer and fall samples. By contrast, reactions to daphniids were seen in equal proportions at all seasons. In C. expleta , most positive results with diaptomids, chironomids, ephemeropterans and zygopterans were seen in fall, but few earlier in the year, whereas reactions with daphniid antiserum were most frequent in spring and fewest in fall. It thus seems clear that, when all instars are considered together, the dietary thrust of each species was directed to different stages. However, the proportions of stages examined in serological samples do not necessarily represent the proportions found in the field, although the distribution of the stages with season obviously is a function of their presence.

To explore this trend further in the sympatric situation, the degree of feeding on each foodstuff was compared for the two Cenocorixa species. Table XLVIII indicates that in fall, when C. expleta showed a high proportion of reactions with all foodstuffs tested except daphniids, markedly more positive reactions with all antisera were seen in guts of this species than in C. bifida , when all antisera are considered together. Conversely, in summer, when reactions in C. bifida guts were generally most frequent (table XLVII) this species showed relatively more positive reactions in guts than did C. expleta for all foods tested, summed. This may be related to the instars present at each season, since the initial analyses showed often

Table XLVIII. Seasonal preferences of <u>Cenocorixa</u> species for different foodstuffs, from serological data.

ANTISERUM	SPRING superior		SUMMER superior		FALL superior	
	sp.	P=	sp.	P=	sp.	P=
Diaptomid	<u>Bi</u>	0.31	<u>Bi</u>	0.00	<u>Ex</u>	0.36
Daphniid	<u>Ex</u>	0.00	<u>Bi</u>	0.00	<u>Ex</u>	0.59
Chaoborid	<u>Bi</u>	0.80	<u>Bi</u>	0.75	<u>Ex</u>	0.37
Chironomid	<u>Bi</u>	0.21	<u>Bi</u>	0.00	<u>Ex</u>	0.19
Ephemeropt	<u>Bi</u>	0.44	<u>Bi</u>	0.00	<u>Ex</u>	0.00
Zygopteran	<u>Ex</u>	0.27	<u>Bi</u>	0.52	<u>Ex</u>	0.40

great discrepancies in proportions of positive reactions in guts between the different stages. Again, the ratio of the stages in samples may not parallel the ratio in the field at each season, so that this trend, while real as far as the serological analyses go, may not be a true representation of the field condition.

Summary of Cenocorixa feeding patterns

Overall results of feeding pattern, as determined by serological gut examination, were given in Table XXVIII (above), and have been re-analysed in Table XLIX to indicate differences between the two species. When data are pooled for instars, lakes and seasons of collection, C. expleta showed relatively more positive reactions with chironomid and daphniid antisera than did C. bifida , although the reverse trend was seen with diaptomid and zygopteran antisera.

These results must now be reinterpreted in terms of differences between instars and species at different seasons and in each lake group, and in the light of information gained from feeding experiments. Thus the difference in feeding on amphipods and chaoborids is affected by the restriction of these animals chiefly to the lower salinities. Feeding experiments indicated that although they did not encounter them in nature, C. expleta took dead amphipods more readily than did C. bifida .

The fact that relatively more positive reactions to

Table XLIX. Differences in feeding pattern between C. bifida and C. expleta in terms of percentage of positive reactions to the antisera listed.

ANTISERUM	SUPERIOR SPECIES	probability (p)
DIAPTOMID	C. BIFIDA	0.1125
DAPHNIID	C. EXPLETA	0.0814
AMPHIPOD	C. BIFIDA	0.5616
CHAOBORID	C. EXPLETA	0.9235
CHIRONOMID	C. EXPLETA	0.0877
EPHEMEROPTERAN	C. BIFIDA	0.6453
ZYGOPTERAN	C. BIFIDA	0.1786
PULMONATE	C. EXPLETA	0.5558
BLUE-GREEN ALGAE	C. BIFIDA	0.5589
MACROPHYTE	C. BIFIDA	0.6808

chironomid antiserum were detected in C. bifida than in C. expleta guts (p=0.09) is not explainable on these terms, as in both species chironomids were the most frequently eaten prey in serological experiments. Although there is little information on the fauna of Lake LB 2, differences in percentages of positive reactions to this antiserum in allopatry and sympatry and between species do not appear to be attributable to differences in abundance of this foodstuff. This is apparent in Table L, which gives percentages of positive reactions for foods present across the entire range of lakes studied. These are compared for each species and lake group, to look for possible evidence of lessened competition for a food item in sympatry, and hence for some clue towards competitive displacement.

For C. expleta , although reactions with chironomid anti-serum were slightly more numerous in allopatry than in sympatry (p=0.45), the reverse was significant for daphniids, ephemeropterans and zygopterans (p=0.00 in each case). However, all these foodstuffs may have been rare in Lake LB 2, limited in abundance by the high alkalinity levels. Data for C. bifida also suggest that the level of feeding on chironomids, represented by the percentage of guts showing positive precipitin reactions, fell slightly though non-significantly in sympatry (p=0.34), but that proportions of guts reacting to daphniid and ephemeropteran antisera increased significantly in the sympatric situation (p=0.00 for both cases), hardly the classic competitive exclusion picture. When diaptomids (not presented in the Table as they do not extend into the more freshwater lakes) are considered, however, highest numbers of positive reactions with

Table L. Percentages of positive reactions to antisera prepared for species common across the entire range of lakes studied, with total numbers of guts tested in both species, divided by lake group.

ANTISERUM	CORIXID SPECIES	LAKES 1	LAKES 2 (sympatric)	LAKES 3
Daphniid	C. bifida		38.4	12.9
	C. expleta	17.5	45.4	
Chironomid	C. bifida		74.4	77.0
	C. expleta	71.1	67.7	
Ephemeropt	C. bifida		29.5	14.0
	C. expleta	16.0	27.7	
Zygopteran	C. bifida		56.9	56.1
	C. expleta	5.2	61.9	
TOTALS (N)	C. bifida		760	456
	C. expleta	294	260	

guts (29.6%) were found in C. expleta from Lake LB 2, dropping by almost 50% to 16.2% in sympatry (p=0.00), when similar results for C. bifida were 20.9% of guts reacting positively. As the food base may be narrower in the highest salinity of LB 2 (chapter II), such a high level of positive reactions of C. expleta there might be explainable by the restricted food available.

Feeding experiments suggested that although with mixed plankton C. expleta took markedly more diaptomids than did C. bifida , in single prey studies both species took diaptomids at an almost equal rate, except for the smallest instars. C. bifida , however, took more daphniids than did C. expleta . These results are not reflected in the data for field-collected corixid gut contents, but with all indirect techniques of gut examination there is no easy way to quantify the positive reactions recorded in terms of amounts of plankters eaten. Thus, a gut containing the body juices of one diaptomid and many daphniids might score positively for each, giving a false representation of the diet, and this is especially true with small food items of which several may be taken in a short period of time. Feeding on larger preys or large dead organisms may result in a truer picture from serological data, but the technique does not allow for discrimination between live and dead preys.

Thus, the feeding pattern varies dynamically with time of year and instars present in any one lake, and any summary can only be of limited usefulness. However, the results overall

indicate carnivory in all instars, with the bulk of the diet being composed of chironomids and zygopterans in both Cenocorixa species, with smaller numbers of other prey. There is thus no strong indication of differences in diet either in the allopatric or sympatric situations, and the species must therefore be considered as potential competitors in the sympatric situation in the moderately highly saline lakes of Becher's Prairie where they coexist.

Gut colour and serologically determined gut contents

Gut colour was noted for 1386 of the corixids tested serologically; these are listed with their gut contents in Table LI. There is no clear correlation of diet with a particular colour. Further, since in most cases multiple contents were recorded for a gut, the colour observed may not be one characteristic of any of these foodstuffs, but a mixture, depending on the amounts of each present. About 44% of all guts were recorded as 'brown'.

The category 'colourless' and often supposedly empty had the largest proportion of negative results for gut contents, although these still formed under 20% of all guts. Low counts of plankters, chironomids and ephemeropterans were recorded in these colourless guts. In the corixids with yellow guts, chironomids, ephemeropterans and zygopterans were relatively important, and diaptomids and chironomids dominated tan guts.

Table LI. Gut colours in relation to serologically determined gut contents of 1386 field-collected Cenocorixa species. Largest percentage underlined for each colour.

GUT COLOUR:	0 none	1 yellow	2 tan	3 red	4 brown	5 olive	n=
ANTISERA	PERCENTAGE REACTING, SHOWING EACH COLOUR						
DIAPTOMIDS	8.8	15.3	21.4	47.6	12.4	7.1	260
DAPHNIID	13.5	16.1	22.7	27.1	28.6	12.5	330
AMPHIPOD			0.9		2.5	1.8	18
CHAOBORID	3.5	3.2	3.6	0.5	2.6	5.4	38
CHIRONOMID	65.5	85.5	80.5	71.9	73.7	80.4	1037
EPHEMEROPT	20.5	34.7	26.4	29.5	22.5	26.8	349
ZYGOPTERAN	57.9	62.9	61.8	52.4	56.0	69.6	801
PULMONATE	0.6		0.5		0.2		3
BLUE-GREEN			0.5		0.3		3
MACROPHYTES				0.5			1
totals	171	124	220	210	605	56	1386

Almost 50% of red guts contained diaptomids, the most marked correlation of diet and gut colour seen. Relatively high amounts of daphniids and ephemeropterans were also recorded in red guts; and among all guts showing no serological reactions with the antisera tested, red guts were fewest. Brown guts, the dominant group, had no distinctive food item prodominating, while the olive guts, forming about 10% of the total tested, had low numbers of positive reactions for plankters. The relatively high proportion of guts in this and the last group for which results of serological tests were negative indicated that the antisera used did not cover the entire range of foods of corixids in the field.

Diets of other corixid species

Data for other corixid species are much fewer than those for the two species of Cenocorixa , and therefore diets are harder to establish with confidence. However, they are of interest, since these other corixid species coexist with C. bifida in the three most freshwater lakes on Becher's Prairie. Positive precipitin reactions with pulmonates, blue-green and filamentous green algae and higher plants were not recorded in any tests. In terms of the percentage occurrence as positive precipitin reactions, zygopterans and chironomids were the major items of diet in every corixid species studied. Among other major foods, daphniids were recorded in over 20% of

C. americana and ephemeropterans in H. laevigata and C. audeni .
Table XXVIII (above) indicates the food pattern for all six
corixid species taken in this study, as determined by
serological analysis of gut contents.

When species were compared using the chi-square test,
Sigara sp. and C. americana showed no trends of difference in
diet. However, results were different and counter-intuitive for
the sympatric but differently sized H. laevigata and C. audeni .
In guts of the small C. audeni significantly more positive
precipitin reactions were seen with amphipod antiserum than in
the larger H. laevigata , and in C. audeni there were also less
reactions to chaoborids, but more to chironomids, than in
H. laevigata .

When results for each corixid species were compared with
those for sympatric specimens of C. bifida in the more
freshwater lakes (table LII) H. laevigata clearly showed a
greater frequency of positive reactions with chaoborids and also
had somewhat more serological evidence of feeding on chironomids
than did C. bifida . In Table XXVIII the highest total
percentage of foodstuffs in the four minor corixid species was
seen in C. americana , with a level about equal to that of
C. expleta although less than that for C. bifida . A level of
200% total foods represents a mean record of two food items per
gut tested.

C. audeni showed markedly more positive reactions with
amphipods than did C. bifida and slightly more with diaptomid
antiserum. However, as diaptomids did not occur in the more

Table LII. Comparison of feeding data for different species of corixids encountered in the study with C. bifida , using chi square tests.

ANTISERUM:	C. bifida versus H. laevigata p=	C. bifida versus C. audeni p=	C. bifida versus C. americana p=	C. bifida versus Sigara sp. p=
Diaptomid	Bi 0.85	Bi 0.60	Bi 0.89	Bi 0.92
Daphniid	Bi 0.19	Bi 0.25	Bi 0.73	Bi 0.89
Amphipod	Bi 0.28	Call 0.00	Cym 0.66	Bi 0.57
Chaoborid	Hesp 0.00	Bi 0.74	Bi 0.75	Bi 0.84
Chironomid	Hesp 0.07	Bi 0.82	Bi 0.73	Bi 0.94
Ephemeropteran	Hesp 0.24	Call 0.16	Bi 0.48	Bi 0.38
Zygopteran	Hesp 0.21	Call 0.64	Bi 0.76	Bi 0.83

freshwater lakes, this reaction may be spurious. There were no clear-cut differences seen in comparing Sigara sp. or C. americana results with data for C. bifida , partly due to the few tests run for these relatively uncommon species (n=11 and 10 respectively), but C. bifida tended to show slightly higher proportions of positive results with almost all antisera tested than did either of these species.

DISCUSSION

Serological techniques rank in sensitivity with the use of radio-active tracers for the study of gut contents (Davies, 1969) and have the advantage of not requiring tampering with the environment. Tests of the antisera indicate that the techniques used were within experimental limits reliable in describing the gut contents of the studied corixids. Davies (1969) found antisera to retain their effectiveness after storage for two years; no sera in the present study were stored for more than 12 months.

Prey homogenates were combined from several related species, sometimes collected from widely separated localities, in an attempt to produce an antiserum with broad specificity for a group rather than for a single species. On hindsight it might have been preferable to have used one homogeneous strain of organisms for each antiserum, trusting to the use of an adjuvant

(Jurin and Tannock, 1972), multiple injections (Proom, 1943) or increased amounts of antigen (Kabat and Mayer, 1961) to spread the specificity. Thus, even specific antigenic material obtained by homogenising genetically identical human cell iso-strains produced 14 different strong bands and as many weaker ones through reactions with the complex mixture of antigens represented even in this uniform source (Brand, 1965). Also, the reactions varied depending on the individual serum-producing animal; thus strength of reaction and number of bands cannot always be equated with strength of the antigenic material tested or quantity of food present.

Quantitation of the precipitin response has been attempted by various authors. Jalanti and Henney (1972) studied radial immunodiffusion techniques to quantify strength of antigens and antibodies, and Mulder et al., (1972) also used single radial diffusion to quantify antigenic proteins, a process now used extensively to measure immunoglobulin concentrations in sera. Preer (1956) attempted to quantify a technique of double diffusion in agar, while Duquesnoy (1973) devised a method of rapid quantitation by electroimmunodiffusion, using discs of filter paper of uniform size soaked in the antisera and placed on agar. However, it seemed inadvisable to attempt such methods in studies of field-collected organisms where there are so many unknowns. Since the corixids seem to ingest a good proportion of each prey caught (chapter IV), the amount of each foodstuff present in the diet will depend on the food item size, and perhaps its specific identity, as well as on how long ago it was eaten; information that cannot be obtained a posteriori.

Therefore, both strong and weak precipitin bands were taken as positive evidence for a food item, and quantitation was based simply on proportions of individuals tested containing that food item, relative to other dietary components.

The main drawback to analysis of the results obtained is common to other indirect methods of dietary evaluation through gut contents, in that predation cannot be distinguished from carrion feeding (i.e. Sutton, 1970); for this reason separate feeding experiments are necessary to substantiate results of all such studies. The difference between predation and scavenging habits indicate very different roles in a community. A third possibility is noted by Fox and Maclelland (1956) who indicate that positive serological results for wireworms in carabid guts might be the result of carabids feeding on the wireworm's predators as much as on wireworms themselves.

The general corixid food pattern which emerges from this study is similar to that revealed by feeding experiments in the preceding chapter. Thus, the differences between fundamental and realised niches are not great. All five genera studied were shown to be largely carnivorous. On first observations C. bifida and C. expleta showed only slight differences in their food spectrum and concentration but these take on greater significance when results are broken down by instars, habitats and seasons. Studies to correlate gut colour with contents indicated a certain discrepancy in results, since about 10% of guts tested, although often strongly coloured, were according to serological evidence empty. Thus perhaps about a tenth of the

diet may consist of untested foods; among this may be algae and higher plants not reacting with the sera used.

Accuracy of the serological tests seems to be fairly high. Thus, under 1% of guts showed a positive reaction to the antiserum prepared for aquatic macrophytes, which, although immunologically inert, was used in many tests to replace the control well of saline used by Pickavance (970).

Similarly low levels of reaction were seen with pulmonate and blue-green algal sera; this indicated that although these sera were reactive in specific tests, the food substances represented did not generally appear in guts examined. It is thus likely that snails and their eggs do not form any regular part of the corixid diet in central British Columbia. However, blue-green material, apparently algal, was seen on one occasion in the guts of several corixids collected in late fall at Lake LB 2, but this was not borne out by gut analysis. Only 17 tests were made of adult C. bifida using serum for filamentous green algae such as Cladophora, and although three of these were positive, the results were too small for any wide significance to be drawn, since this antiserum was also weak in strength tests.

A major source of discrepancy between field observations and serological gut data is seen in the relatively high number of guts from freshwater lake collections reacting with the diaptomid antiserum (4.7% for C. bifida and up to 10.0% for the less common corixid species studied). It seems most likely that in this case the specificity of the serum was broad, probably as

a result of its preparation using an adjuvant, and the results
are reactions to related crustaceans, possibly the cyclopoid
copepods common in the freshwater lakes. By contrast, results
for amphipods and chaoborids in the higher salinity lakes were
at a much lower level (around 1.0%) and may be put down either
to experimental error or to the occasional presence of both of
these forms in certain of the higher salinity lakes (chapter
II). The greater proportion of diaptomids in guts of C. expleta
than in C. bifida overall is similarly connected with
distribution of the two Cenocorixa species and the food item.

The examples where reactions to chaoborids, amphipods and
diaptomids contrast with distribution patterns emphasise the
need for caution in formulating summary statements about dietary
preferences. However, geographic distribution cannot be invoked
to explain why C. bifida ate significantly more daphniids and
ephemeropterans in sympatry than in allopatry, since both were
apparently abundant in all lakes studied.

In alkaline lakes, the fauna is apparently less diverse
(chapter II) and because of the general absence of seasonally
appearing masses of aquatic plants, most organisms in these
lakes may be generally less dependent upon this for concealment
and breeding. Numbers may therefore be more constant from season
to season, as was seen in the plankters at least. Since there is
a greater variety of foods in the more freshwater lakes than in
the more alkaline ones, individual items of food may also figure
less frequently in the diets of corixids collected there.

Most tests focussed on a particular lake group rather than

on overall data. A further area of possible bias investigated was the difference between diets of _Cenocorixa_ species collected at different times of year. _C. bifida_ fed significantly more on diaptomids, chironomids and ephemeropterans in summer than at other times of year, whereas _C. expleta_ fed significantly highest on these items in fall. Examining the situation with diaptomids in more detail, significantly more were consumed by _C. bifida_ than by _C. expleta_ in summer but the reverse tendency, non-significant, was seen in fall. Reasons for such seasonal differences may lie in the differing abundance of organisms in different seasons. Plankton samples indicate that both daphniids and diaptomids were frequent all year in the Becher's Prairie lakes, although showing a summer peak (chapter II). However, observations at Lake LB 2 indicated that in spring diaptomids were not evident, although abundant later in the year. Perhaps the abundant diaptomid prey on Becher's Prairie may have been of differing availability to the two species at different seasons in some manner. If the pattern is not explainable by the fact that many of the _C. expleta_ examined came from Lake LB 2, an alternative explanation might be that _C. expleta_ may have fed chiefly on, for instance, dead and dying plankters, which may have been commonest in the fall. Results from feeding experiments agree in part with this, but only subjective observations on mortality levels of diaptomids in the field at different times of year exist to corroborate the hypothesis.

Alternatively, if, as feeding experiments indicate, adults took relatively less diaptomids than did juveniles and if summer samples chiefly contained _C. expleta_ adults and _C. bifida_

juveniles and the fall samples vice versa, the same results could be explained. Among those examined serologically, adults of both species made up 17% of summer samples, but in the fall 92% of C. bifida were adult, but only 36% of C. expleta , a fact perhaps related to the third summer generation seen in the latter species. Thus the conditions to support the findings are partly consistent with the third hypothesis. It would seem likely that all three suggestions have some basis in forming the observed summary feeding pattern for each species at different seasons.

Other foods seasonally evident in the guts may reflect differences in the activity of prey or predator with temperature, thus explaining the cases of C. bifida showing most evidence of feeding on chironomids and ephemeropterans in summer. The picure may be further complicated by prey organism emergence patterns and size changes with growth.

There was some indication that in each species different instars had their preferred food item or items. Thus if one instar predominated in a collection, this might bias overall results towards the preferred food of that instar. From Table XLVI listing such instar food preferences, it could be seen that the diet increased in complexity with increasing stage, starting in young nymphs with planktonic food, chironomids and zygopterans and expanding to include other less important items such as chaoborids and amphipods in larger instars. However, in the smallest instars small volumes of foods may not show up in the serology tests. The pattern for greater feeding by one or

other species on different foodstuffs showed no consistent trend between instars, but it nevertheless represented a real partitioning of the food spectrum. Overall, there was a generally greater level of feeding seen in C. bifida over C. expleta for the foods tested.

A 'plateau' level of feeding on most foodstuffs was reached earlier in C. expleta than in C. bifida . This is likely to be due to the slightly larger size (Scudder, 1966) of C. expleta and its more robust palae at all stages, permitting more efficient capture and handling of a wider variety of and larger foods. However, above this threshold size, C. bifida was generally superior to C. expleta in the amounts of most foods taken. Thus from the third instar up C. expleta loses its superiority in terms of percentages feeding on both plankters and benthic naiads, to C. bifida .

Sex differences in feeding were not usually marked with Cenocorixa , but males tended to show more positive evidence of feeding than females in every case. For C. bifida those foods present almost equally in each sex played little importance in the diet overall, but those foods showing little sex difference in C. expleta males and females include daphniids and zygopterans, which comprised on average 30% or 40% of the diet, or about six times as important as those items mentioned in C. bifida . Sex differences in feeding pattern may thus bias results more significantly in the latter than the former species.

Results for other species of corixids sympatric with

Cenocorixa indicated that H. laevigata may eat more chironomid larvae, and C. audeni relatively more amphipods and chironomids, than other species. These two corixid species are the most disparate in size. The feeding pattern indicated, if real, may be related to habitat or swimming behaviour differences, suggesting that H. laevigata may frequent midwaters and C. audeni predominantly the benthic areas. H. laevigata showed rather more positive reactions with ephemeropterans and zygopterans than in Cenocorixa species; this may be related to its larger size, and hence greater ability to capture these larger preys. An alternative hypothesis is that, being larger, H. laevigata guts contain relatively more food than those of Cenocorixa which might mean a greater variety of food at any one time. Thus a foodstuff might figure more frequently in H. laevigata than in Cenocorixa although in volume relative to the other foodstuffs it might comprise equal amounts; this information was not available from the serological data on guts examined.

C. audeni showed more evidence of feeding than did C. bifida on amphipods and perhaps also on daphniids. This might be linked either with adeptness of capture, or with the small sample size, and reinforces the suggestion made earlier, that C. audeni may be more benthic-oriented than H. laevigata or C. bifida . Results with chironomid larvae were inconclusive in this regard, but it should be remembered that in the higher alkalinity lakes these were usually found in the mud or water column, whereas in the more freshwater bodies they were equally abundant among the aquatic vegetation and therefore perhaps more

visible to a vegetation-perching corixid.

Thus in sympatric situations with potential for interspecific competition some corixid species are feeding on the same items. However, the concept of 'refuge' species, in the sense of Reynoldson and Bellamy (1973) may be valid here, as C. audeni may be using amphipods, and H. laevigata chaoborids, as refuge items. These food organisms are not necessarily the preferred item, but are rather those for which the species has a clear superiority in capture and feeding when competition becomes intense or food limited. They thus allow more effective partitioning of the resource. However, evidence of their use is not marked in the lakes studied, where in general food seems superfluous to corixid needs. Thus although there is evidence of much overlap of corixid diet, there is no corresponding evidence for competition.

Finally, with increasing evidence of differences between instars, sexes, habitats and seasons, it becomes progressively less meaningful in the present context to talk of a 'typical' corixid diet, since all these variables interact to produce the summary. Thus, relatively small samples in experiments such as those of Young (1973) could produce very different results depending on the distribution of instars in them or even on the dates of sampling. In the present results, obscuring of the true dynamic pattern necessarily results from considering the corixids collected under three main seasonal headings alone, but logistics of time and facilities preclude a fuller investigation of a narrower spectrum of organisms. With a greater knowledge of

the background conditions of the habitat, such results could be
obtained, but in an environment such as that of Pecher's Prairie
the situation may vary significantly from year tc year, so that
conclusions drawn from the surveys of one season may not be
valid for the next.

CHAPTER VI. DISCUSSION

The concepts of competition and coexistence provide rich grounds for misunderstanding, due largely to differences in definitions and usage of these and other terms central to the problem, such as 'niche', 'competitive exclusion' and 'sympatry'. The historical development of these concepts and differences in definitions have already been reviewed in Chapter I. This section will discuss some of the field studies of competition and the problems they attempted to solve. These are considered here because of the light they may throw on the Cenocorixa problem.

Many laboratory studies suffer from founder effects or genetic drift in the small, often inbreeding populations involved (e.g. Dobzhansky, 1962). They also show more regular conditions than are found in most natural environments, and are thus unsuitable for direct comparison with field situations.

In the present discussion, only direct interaction is considered as evidence of competition, following the definition of Crombie (1947) rather than the Darlington (1972) concept of extended competition. The term 'niche' is also considered primarily non-quantitatively, as a composite of function and habitat, with the realisation that it would require considerably more study to elucidate all the factors that may be relevant.

As Birch and Erlich (1967) point out, "...we know nothing whatever of the antecedents of most species for thousands of years...". Certainly nothing is known of the past history of

Cenocorixa in central British Columbia. Past competition can be invoked as a reason for present distribution, but never falsified; thus ongoing competition should be studied where possible, rather than assessing present distribution patterns in the light of previous competition.

Previous field studies of aquatic habitats, which form well-defined ecosystems in general, have included several dealing with zooplanktonic organisms. Amongst these, Goulden (1966), working on coexistence of moinids, found little difference between niches to account for the apparently sympatric distribution. Sandercock (1967) looked at coexistence of diaptomids in one lake, and suggested coexistence was due in that case to the use of different ecological niches in sympatry. Size differences between the species lessened competition; there was also vertical segregation in the water column in summer, and some seasonal differentiation of abundance peaks.

Stahl (1966) studied coexisting species of Chaoborus in many water bodies. Among more general factors which might permit coexistence, ecological niche differences were not generally recognised as important, and the chief factor permitting coexistence was considered to be unrestricted resources. Considering only the aquatic (non-reproductive) phase, numbers were generally effectively reduced by fish predation, by crowding on the bottom and by weather patterns at emergence for the populations he studied, so that they never reached a level where competition was severe. In contrast to this study, Swift (1974) found that in the absence of fish predation development

of Chaoborus may be retarded by a shortage of food, and a two-year life cycle imposed on chaoborids in sympatry, rather than the exclusion of one species. His findings resemble those of Wallace (1974) who found that larval development of Drosophila was prolonged in overcrowded cultures; similar results are common in insect laboratory studies.

In general, many of the previous studies on aquatic organisms often seem to define the niche in terms of food, rather than other environmental parameters.

There has been considerable work on competition in birds, since Lack's support of Gause's views at the British Ecological Society's meeting of 1944, dealing with the biology of closely related species (Hardin, 1960). For instance, Orians and Horn (1969) studied similar-sized blackbird species in sympatry around potholes in sagebrush country, reasoning that in fluctuating environments little is known about how much overlap is required before competitive exclusion need be expected, although the principle is fairly well understood in the laboratory. Overall food overlap was high at all times for three of the four species, enough to favour the development of interspecific interference competition (territorial behaviour) between two of these. Thus, when foraging in the same habitat at the same time, they obtained approximately the same diet, and could be classed as 'fine-grained' in the sense of MacArthur and Levins (1964). The data supported the suggestion that under competition in a patchy environment a species will decrease the number of patches foraged in, rather than the number of prey

types taken (MacArthur and Pianka, 1966). Here again, the fundamental and realised niches were clearly defined in terms of habitat rather than role.

In a rather similar study Catchpole (1973) looked at two warblers and clarified the ideas of 'sympatry' in their context; he identified horizontal, spatial and seasonal segregation in breeding and partly in feeding. The species were effectively largely allopatric, although both inhabited the fringes of ponds. With such a result, it is tempting to postulate past competition.

In a recent investigation, Enders (1974) found that orb-web spiders were segregated vertically in spring and early summer, but when the population was lowered by predation, the species of Argiope were able to coexist in later summer. Competition was both by exploitation and interference in the earlier stages.

Zaret and Rand (1971), pointing out that competitive exclusion was most often used as an explanation of present niche separation of sympatric species and that this was impossible to disprove, considered it best studied by collecting, as did Orians and Horn (1969), data on niche overlap in the absence of information on, or preconceived ideas of, competition. They found that tropical stream fishes sharing similar habitats had most distinct food preferences, and found also a greater niche overlap in the wet season when food was abundant, than in the dry season when species and numbers of preys were both fewer. This is in conflict with some other findings, but more resembles Reynoldson and Bellamy's (1971) concepts of refuge prey species,

whereas Emlen (1966) predicted mathematically that predators would switch from specialised to generalised feeding in times of scarcity (confirmed by Sprules in 1970).

Most of these studies predicted habitats from stomach contents - the realised niche evidence - without an independent measure of what food organisms may constitute the fundamental niche of the species. Similarity in diet need not necessarily mean similar feeding-places or behaviour; thus, as the functional and distributional niches may not overlap, competition need not necessarily occur. Therefore independent feeding experiments, despite their obvious disadvantages and artificiality, are often necessary to discern the fundamental niche and to interpret the field results behaviourally and in terms of preference. In this way, laboratory studies of Kear (1962) on finch feeding behaviour and its evolution with development, throw light on many field study situations.

In contrast to the rather clear-cut situations considered above, there are observations of certain insect groups where several species may coexist, apparently in complete sympatry. DeBach (1966) and Miller (1967) reviewed detailed work by Dempster and colleagues on coexistence of broom fauna. Ross (1957) describes another such situation where sibling species of leaf-hoppers (Erythroneura lawsoni s.l.) coexisted apparently without competition on sycamore trees . Trees with few hoppers did not show greater species diversity than those supporting high populations, indicating a general lack of competition. Perhaps each species has a slightly different ecological

optimum, but fluctuations in weather and other factors tend to favour each in turn. Thus despite synchronous breeding patterns and identical feeding habits in these leaf-hoppers, the situations appear not to be resource-limited; each tree represents an ecosystem with superfluous food. Perhaps breeding is inadequate to exploit the situation in the time period when leaves are on the trees. These and other field examples indicate that competition may occur between siblings, but may not necessarily reach a rapid exclusion end point; there is thus field evidence for the mathematically predicted coexistence (Miller, 1967).

COMPETITION IN FLUCTUATING ENVIRONMENTS

Some ecological studies suggest that many species may have very plastic genetics, to enable them to adapt rapidly to a changing environment (Birch and Ehrlich, 1967). Although the idea of competitive exclusion is fundamentally an evolutionary concept, in studies of competition there is often a tendency to look for an end-point situation - the exclusion of one or other species - without investigating the possibility of ongoing competition. Weatherley (1963) suggests that among the indicators of ongoing competition are factors such as depressed growth and reproduction which may be observed on experimental reduction of the population density. However, this is applicable to interspecific and intraspecific competition alike, as many studies on trout show (i.e. Reynolds et al., 1964).

In any environment, competitive displacement may still actively be in progress (DeBach, 1966). In a fluctuating environment the outcome of competition may be much delayed, or even reversed from time to time; competitive exclusion may often depend on reproductive inequalities (Miller, 1967), and changes in environmental situations may reverse the advantages. Ideas of a time scale for such a process, while influenced by the reproductive patterns and life spans of the species under consideration, remain vague.

In temperate areas, large-scale physical and climatic changes have occurred within the past 20,000 years and there is evidence of continuing climatic change, either semi-cyclical, or now following an irreversible direction (Bryson, 1974). Thus the stresses in a changing habitat will continually be altering, and affecting the inhabitants differently. On Becher's Prairie, Lake Lye has occasionally separated into two parts in exceptionally dry years; other lakes have diminished in volume and area, and conductivity has fluctuated greatly (Scudder, 1969b). There seems also to have been a general rise in water level in many lakes about 20 years ago, seen by the stands of dead aspens in many lake shallows (Cannings, 1973). The effects of climatic change would normally be more marked in closed systems, such as the Becher's Prairie lakes, than in lakes or other aquatic habitats linked by streams to other systems.

Further, in a continental climate such as that of the central interior of British Columbia, there is a pronounced winter break separating relatively short growing seasons. This

will not only cause great changes in conditions in the lakes as a result of freezing over, i.e. changes in salinity, oxygen content and so on, but it may also lead to the components of competitive exclusion being reduced in effectiveness, especially where the life span of the organisms involved is shorter than the periodicity of environmental variation. The process of competition may effectively start anew each year with many groups of invertebrates, including corixids, which usually overwinter as adults (Martin, 1972) and eat little or nothing below 5 C (Jansson and Scudder, 1972).

SUMMARY OF THE FINDINGS FOR C. BIFIDA AND C. EXPLETA

The present study was centred around the problem of coexistence in closely related corixids. The aim of the study was basically to establish fundamental and realised niches for C. bifida and C. expleta . A reduction of the fundamental niche in sympatry is an essential for the demonstration of a competitive situation (Miller, 1967), but it need not be an indicator of competition. Careful methodology is needed in field studies to show that two species are ecological homologues in the first place, a prerequisite for an exclusion outcome (Connell, 1961).

Lake LB 2 can essentially be considered as allopatric for C. expleta since no C. bifida were detected there during the present study, and the Becher's Prairie lakes Greer, Rock and East are similarly allopatric for C. bifida . The life of the corixids in these lakes may thus be studied and compared (a) with where they occur in sympatry on Becher's Prairie (Lakes Barnes, Lye and Round-up), and (b) with laboratory results, to determine first whether such data indicate ecological identity between the species, and second, the differences between fundamental and realised niches, if any, for each species. This discussion will analyse the major topics studied, in terms of physiology, habitat and feeding preferences of each species.

First, in terms of their osmotic and ionic physiology, C. expleta , which has not been found in lakes in central British Columbia below 5000 umhos cm^{-1} conductivity (Scudder,

1969) was essentially allopatric in the highest salinity studied (Lake LB 2). C. bifida was allopatric in lakes below 2000 umhos cm^{-1}, while both species occurred sympatrically on Becher's Prairie lakes with waters of from 6000 to 12,000 umhos cm^{-1} mean conductivity. Other corixid species occurred in small numbers in most lakes, but bred in sympatry with C. bifida only. The lakes investigated were generally similar in ionic content, but differed markedly in conductivity. Topping (1969), however, points out that in each lake there is a significant seasonal variation in conductivity.

The different distribution of the Cenocorixa species in the upper salinity ranges appears to be at least partly due to differences in physiological tolerance. Scudder et al., (1972) have shown that both species of Cenocorixa have typically freshwater ionic-osmotic balances, and live equally well in experimental situations up to 20,000 umhos cm^{-1}. However, C. expleta can survive in up to 30,000 umhos conductivity, whereas C. bifida cannot.

Savage (1971) has described the succession of corixids with increasing salinity in saline lakes in Cheshire, with a similar conductivity range to those studied here, of 500 to 22,000 umhos cm^{-1}, but he did not adduce reasons why salinity per se should be the controlling factor. By contrast, Macan (1938, 1962) has shown habitat preferences in corixids which do not appear to relate to conductivity or salinity, but his lake series did not extend into the range of salinities covered here. Istock (1973) remarks that for this very reason of habitat preferences,

corixids are interesting for studies of species interactions.

While C. expleta does not naturally occur in the low salinity lakes, experiments by Scudder et al. (1972) suggest that adults have the physiological capacity to do so. In the present study, C. expleta oviposited in laboratory conditions in water of around 1100 umhos cm^{-1}, and the eggs hatched and development proceeded successfully to the second instar. Scudder et al. (1972) thus suggest that ecological interactions may be among the factors that exclude this species from the most freshwater habitats.

In summary, with respect to physiological aspects of the niche, there is evidence that the fundamental niche of both species should encompass the entire range of the lakes studied. However, the realised niches indicate a distinct restriction of this, with absence of C. bifida from highest salinities, and of C. expleta from the lower salinity water bodies.

When selecting the study area on Becher's Prairie, care was taken to choose lakes with similar depth, area and shore development and major ionic composition. Thus there were minimal differences in substrate and temperature among the physical parameters. However, habitats were rather diverse, as submerged macrophytes were absent from lakes of 6000 umhos cm^{-1} and higher on Becher's Prairie, namely lakes Barnes, Lye and Round-up, although all lakes on Becher's Prairie had occasional fringing patches of Scirpus and Juncus. The lack of submerged vegetation in the saline lakes produces a simpler, less heterogenous environment with fewer hiding-places and probably less spatial

separation of corixids. This may permit potentially more interactions between species and instars, but it was just in these more saline lakes that the species were sympatric. Macrophytes were seen in Lake LB 2, but here they formed isolated clumps rather than a continuous mat.

Since the presence of aquatic plants apparently depends upon both salinity and ionic content (Seddon, 1972), salinity may thus be indirectly responsible for major alterations of the environment, making it less complex in the more saline lakes. Should preferences of the Cenocorixa species for weedy or bare substrates differ, there might be an indirect as well as a direct influence of alkalinity upon their distribution.

In the investigation of habitat preferences, Scudder (1966) has shown that C. expleta oviposited preferentially on solid substrates in captivity and in the field, whereas C. bifida seemed to prefer to lay eggs on surfaces such as plant stems. Thus C. expleta may be absent from weedy areas and lakes because the preferred oviposition site is absent or covered over. Substrate. However, laboratory evidence in the present study indicated that the difference is not clear-cut, for most C. bifida , whether from weedy or weedless lakes, oviposited on the bottom of the containers rather than on the plastic screening provided. Walton (1943) has shown that differences in oviposition site may influence development rates through micro-environmental differences, eggs laid on the bottom developing relatively slower than those laid higher in the water column. However, more definite experiments on the ovipositional aspects

of the fundamental niches of C. bifida and C. expleta need to be carried out.

Habitat preferences for each species of Cenocorixa were investigated in the higher salinity lakes on Becher's Prairie where both Cenocorixa species were sympatric. A higher proportion of both adults and nymphal stages of C. expleta was recorded midlake than inshore. Similarly in Lake LB 2, C. expleta appears to occur both inshore and in deeper waters (Scudder, personal communication). However, C. bifida in the more freshwater lakes was rarely taken midlake, and most surveys suggest it is chiefly confined to inshore areas. Dispersal between and in water bodies might account for some of the midlake adult sightings, but would not affect observations of juveniles in midwaters, nor should it affect ratios of the species if equivalent dispersal can be assumed for each. Thus the pattern seen may indicate a more widespread habitat for C. expleta than for C. bifida . The fundamental niches in terms of habitat of the two species were not directly studied here in the laboratory, but by extrapolation from the evidence in different lakes, it would appear that for C. expleta the fundamental niche is wider than that for C. bifida , and further, that the realised niches are not markedly different in allopatry and sympatry.

In Lakes Barnes and Lye there was a generally greater abundance of C. expleta on bare shores with firm silt or gravel, and offshore. On the other hand, C. bifida was more abundant over soft mud, among Juncus or flooded twigs. In sympatry,

therefore, C. expleta prefered the less diverse habitat and somewhat deeper water, although these sympatric preferences were by no means absolute. In summary, all habitat studies indicated evidence for a wider range of habitat and water depth preferences in C. expleta than in C. bifida , but there is apparently little or no reduction of the fundamental niche in sympatry.

Feeding requirements may also influence habitat selection by different corixid species. Benthic organisms are generally restricted to the littoral regions, where corixids also predominate, but in this area planktonic organisms varied considerably in abundance , largely as a result of wind and wave action. While biomass of invertebrate organisms appeared relatively heavy and sustained in each lake, there were differences in faunal composition.

Jansson (1971) has suggested, however, that dietary deficiencies may occur at certain times in the lakes, and bring about the ovarian arrest that is observed in midsummer. Following Rawson and Moore (1944) he correlated primary productivity with conductivity in saline lakes, and suggested that increased production of prey organisms might allow more corixid generations in the more saline lakes, where ovarian arrest occurred in August rather than in early July as in the more freshwater lakes. However, the present studies indicate that, if anything, there was more phytoplanktonic primary productivity in the more freshwater lakes than in the saline lakes. Much of the primary productivity in the higher salinity

lakes may come from epipelic and benthic blue-green algae, and in the more freshwater lakes from submerged aquatic macrophytes and their associated green filamentous algae. Clearly, the correlation of conductivity and productivity is not simple in lakes of the study area.

Much recent work, notably that of Parsons and colleagues (Parsons et al., 1972; LeBrasseur and Kennedy, 1972; Barraclough and Robinson, 1972) has shown that there may be no correlation between primary production and standing crop. Greater algal production following enrichment of a water body may not show a significant increase in standing crop since there is often a compensatory increase in consumers, especially among the faster-developing cladocerans and rotifers. Thus, if standing crop is to be used to assess productivity, it is best to characterise a lake by repeated samples of zooplanktonic biomass, especially in the absence of higher predators.

Volume measurements (Chapter II) suggest an equivalent level of zooplankton biomass averaged over the season for all lakes, so that productivity in terms of food abundance is apparently not limiting. This is further indicated by comparing Round-up Lake and Lake Lye, where despite great differences in plankton and corixid biomass, development of similar numbers of corixid generations occurred, and at a similar rate (Chapter III). Quality of food is more likely to be a significant factor affecting corixid distribution and reproductive success.

Thus C. bifida is able to survive and breed both in allopatry and when sympatric with C. expleta , and it may be

that the quality of food is greater in the sympatric lakes, resulting in more extended breeding. If the absence of C. expleta from the low salinity lakes is not owing to salinity or other factors so far considered, it is possible that some aspect of the feeding requirements is responsible. The major part of this study was in fact concerned with investigating what organisms both sibling species would eat, as a measure of their fundamental niches, and what they had eaten in the field, using evidence from serological examination of guts, as an indication of the realised niche of each species.

The present study represents the first sophisticated demonstration that many of the Corixidae are in fact carnivorous. Serological analyses of gut contents of six species in five genera, supplemented by data from extensive feeding experiments using preys singly or in combination, showed the predatory and scavenging habits to dominate. Levels of feeding on plant material were at best low, and over half the specimens tested from each species contained evidence of chironomid and zygopteran remains in the guts, with smaller amounts of other lake invertebrates. This is a new finding for Cenocorixa , since previous workers (Jansson and Scudder, 1972) have noted feeding to be chiefly on diaptomids.

The results could indicate food limitation in the lakes studied, forcing the corixids to turn to a carnivorous diet; but if so, one would expect plant feeding to be more important in corixids from the more freshwater lakes where plant material was abundant and where several species of corixids coexist. That the

feeding pattern is not peculiar to alkaline lakes of central British Columbia is indicated by the fact that Cenocorixa blaisdelli (Hungerford) collected in the moist coastal climate again took animal food in experiments. Despite high densities of corixids in all lakes, mud populations and emergences of chironomids remained high (Cannings, 1973), suggesting that these foods, like the plankters, were not limiting. Results suggest that there is no shortage of potential food in the lakes studied.

In feeding experiments C. expleta markedly preferred dead over live foods, a factor not demonstrated in C. bifida (Figure 15). However, live plankters and chironomid larvae were more often taken by C. bifida than by C. expleta . Although in a sense artificial, feeding experiments help to delimit the dietary components of the fundamental niche of each species. However, the ultimate test of the effectiveness of a laboratory-determined diet must come through successful rearing of the species on it for several generations, as was done by Jansson and Scudder (1972) and Peters (1962).

In the experiments of Hungerford (1917) and Griffith (1945) laboratory feeding was less than successfully controlled through the very nature of the tested diets, which may have contained many types of organisms, all potentially available to the corixids. For long-term rearing experiments with a single diet axenic cultures of food species must be used to obtain unequivocal results. Peters and Ulbrich (1973) autoclaved mud and fed this plus branched algae to Trichocorixella, but no

information is given on the algal source, nor of the possible dead organisms contaminating the mud.

In a synthesis of the findings of the last two chapters, Table LIII compares results of feeding experiments and serological gut analyses of the feeding patterns of each Cenocorixa species. The major difference between these results is in the high proportion of guts reacting positively for chironomids and zygopterans compared with importance of these items in feeding experiments. To account for this, major predation may occur on zygopteran eggs which are inserted in submerged plant stems; there may similarly be much predation on very young stages of chironomids which are extremely abundant in all lakes studied. Further, the adjuvant-produced chironomid antiserum is likely to react with Aedes larvae, which were also abundant in the studied lakes. Experiments offering a choice of preys suggested also that capture success of chironomids was greater than that of plankters, although both elicited a strong predatory response. Whatever the explanation, there is apparently a strong emphasis on chironomids and zygopterans in the field.

Laboratory and field data show fairly close correspondence in the order of preference of other food items, except for those foods offered experimentally but not normally available in the field. Both indicate high acceptance of planktonic organisms in both species, and generally more food diversity in the diet of C. bifida than in C. expleta . This greater food diversity is indicated by the higher values of 'all foods' (not listed) by

Table LIII. Feeding preferences of <u>Cenocorixa</u> species in experiments and from serologically determined gut contents. Results expressed as percentages feeding (experiments) and percentages of guts containing the foodstuff (serology). For feeding results, unweighted means were taken of dead and live organisms results.

|	<u>C. bifida</u>		<u>C. expleta</u>	
FOOD ITEM	FEEDING (%)	SEROLOGY (%)	FEEDING (%)	SEROLOGY (%)
Diaptomids	23.8	6.6	18.0	11.4
Daphniids	20.0	12.6	17.1	14.3
Amphipods	13.9	1.8	13.4	0.0
Chaoborids	3.0	1.1	11.9	0.7
Chironomids	18.1	33.5	16.7	34.8
Ephemeropterans	3.6	10.5	11.6	10.5
Zygopterans	11.6	25.1	11.3	28.0
Others:	6.0	8.8	0.0	0.3

both methods. This may be related to prey organism distribution, as C. bifida has a wider distribution pattern on Becher's Prairie than C. expleta . The latter may then be said to fall into an included niche within the wider one of C. bifida , and, if competition is to result in coexistence rather than exclusion of one species, in theory the resource of the included species should be more specialised.

To avoid complication of the feeding pattern through pooling all results, serological data were subdivided so that the sympatric lakes, in which habitats were relatively uniform and plant masses were absent, were studied separately from the allopatric lakes. Significantly more C. bifida and C. expleta took daphniids and ephemeropterans in sympatry than in allopatry, and significantly more C. expleta contained diaptomids and zygopterans in allopatry than in sympatry. It thus seems that both species concentrated on certain key food items when in sympatry. This does not apparently entirely reflect faunal differences between lakes, as daphniids did not appear to differ markedly in abundance between lakes, although ephemeropterans and zygopterans were perhaps more prevalent in the three higher and the three lower salinity lakes respectively (Chapter II). Results of serological experiments are summarised, and contrasted with distribution of major potential foods, in Figure 20.

In summary, the distribution patterns of prey organisms are unlikely to account for the preference of C. expleta for diaptomids in allopatry, and that for both species for daphniids

Figure 20. Summary of occurrence of food items in the field, and percentage of guts of C. bifida and C. expleta containing serological evidence of items.

A= occurrence in low salinity lakes (C. bifida only), b= occurrence in moderate salinities (C. bifida and C. expleta sympatric), c= occurence in high salinity (C. expleta cnly).
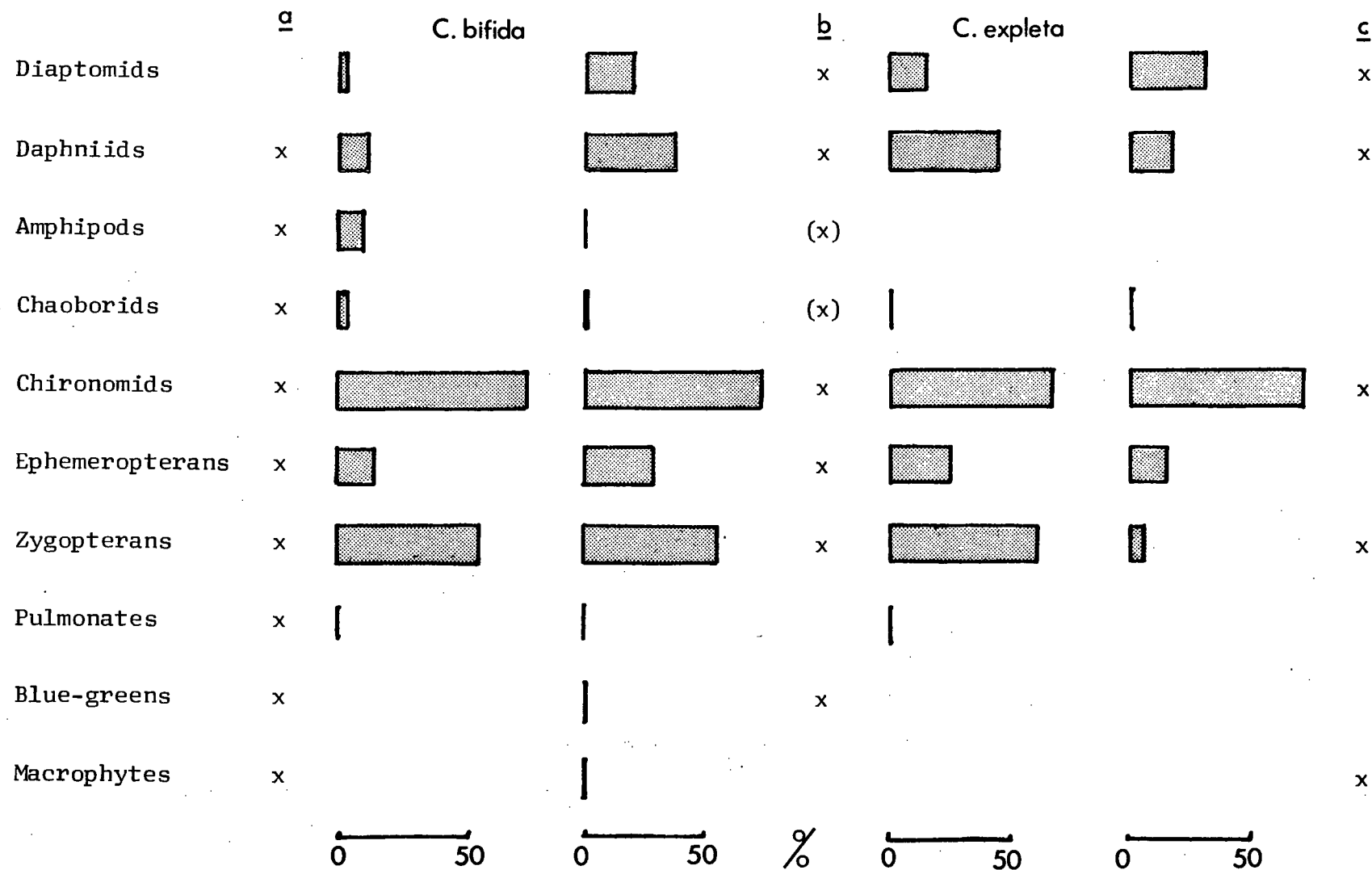
in sympatry; it is also doubtful if feeding pressure on ephemeropterans and zygopterans could be explained solely by habitat preferences.

The results from the study of the species of C̲e̲n̲o̲c̲o̲r̲i̲x̲a̲ in sympatry afforded the best evidence for the existence of differences in the feeding niche. Thus, in spring (Tables XLVII and XLVIII) more C̲. e̲x̲p̲l̲e̲t̲a̲ than C̲. b̲i̲f̲i̲d̲a̲ contained daphniids, whereas in midsummer the reverse was true. This change was not immediately explicable in terms of prey abundance. Perhaps copepodites and nauplii of diaptomids were most abundant by midseason, providing an alternative foodsource. Similarly, C̲. b̲i̲f̲i̲d̲a̲ took more chironomids and ephemeropterans than C̲. e̲x̲p̲l̲e̲t̲a̲ in summer, but the reverse was seen in fall, indicating another seasonal shift in emphasis on foodstuffs. This might be because of the different proportions of instars of each species present at different times of the year, resulting in the changing expression of overall food preferences for each species at different seasons. Changes in the day to day dynamics of the field environment affected prey densities inshore and proportions of developmental stages present at any one time.

However explained, these different and changing preferences of each species for different preys indicate the difficulties of summarising feeding patterns. Nonetheless, the results of feeding studies indicate similar, although not identical, fundamental niches for the C̲e̲n̲o̲c̲o̲r̲i̲x̲a̲ species, and there is some evidence for a more restricted, or specialised, realised niche of each in sympatry.

When life histories are considered, in the more freshwater lakes C. bifida , H. laevigata , C. audeni , C. americana , and Sigara sp. breed in sympatry. Of these, C. audeni is smaller than the numerically dominant C. bifida , while C. americana is somewhat larger, and H. laevigata is markedly larger and more robust. All produce one generation per year in these lakes.

Hutchinson (1959) points out that in corixids with similar life histories, the young of larger species potentially compete with the adults of smaller forms, whether for food, space or other factors. Martin (1970) suggests that in sympatry larger species usually develop slower, but start earlier. However, this would appear to minimise any selective advantage that might be obtained, and one would expect rather the opposite, that the advantages of size differences would be enhanced by simultaneous breeding, or even by earlier breeding of the larger form.

Differences in timing of breeding season would most logically be expected in the cases of similarly-sized, sympatric species, and in the more freshwater lakes on Becher's Prairie this was in fact seen, for Sigara sp., which was very similar in size and appearance at all instars to C. bifida , started to breed markedly earlier than the latter. However, in the more saline lakes where C. bifida and C. expleta coexist, such a staggering of breeding pattern was not obvious, although Jansson and Scudder (1974) found a time-lag of about one week between the species at the beginning of the season. Thus, there is no evidence for competitive interaction having greatly influenced the timing of breeding between the Cenocorixa species in

sympatry.

DeBach (1966) suggests that non-competing animal species should not show differences in abundance between allopatry and sympatry, other factors being equal. However, this did not prove to be a useful criterion in the present study, since the abundance of the corixids varied enormously in and between lakes, and in no regular manner. This was especially obvious when pairs of lakes with similar chemistry (Rock and Greer; Lye and Round-up) were compared. Certainly, numbers of C. expleta were apparently much lower on Becher's Prairie where they are sympatric with C. bifida than in Lake LB 2, where C. bifida cannot survive all through the year. However, C. bifida was no less abundant in sympatric lakes in general than when not coexisting with C. expleta . In the freshwater lakes the numbers of C. bifida fluctuated greatly (Chapter III). Therefore these abundance data give no clear indication of any competitive situation in sympatry.

The evidence so far amassed on the ecological relationships of C. bifida and C. expleta may now be summarised. As far as their fundamental niches are concerned, C. bifida and C. expleta have been shown to differ in osmotic physiology (C. expleta is able to tolerate higher salinities); habitat (C. expleta generally ranging wider in depth, substrate and vegetation than C. bifida) and to some extent in feeding patterns (C. expleta but not C. bifida preferring dead to live foods). The studies thus show that the species are not ecological homologues: they do not occupy the same niche.

A complex pattern of variation, particularly in feeding behaviour, has thus emerged for the sibling Cenocorixa species in the lakes studied; this is to be expected as prey abundance and availability also fluctuate, with marked peaks of plankton abundance and definite periods of larval insect availability. The experimental work provided evidence that, although the same prey items were accepted by both C. bifida and C. expleta , the species often differed in their rates of acceptance of many preys.

Jansson (1971) and Jansson and Scudder (1974) have suggested that dietary factors may regulate ovarian arrest and hence population growth in Cenocorixa . Since all lakes studied are eutrophic in biotic potential if not in chemical data (Cannings, 1973) and limitations in abundance of food organisms are not apparent, quality rather than quantity of food may indeed be important. In the sympatric lakes the plankton is characterised by diaptomids, which have been shown to be a relatively favoured item of diet of both species of corixid. These food organisms have a relatively higher calorific value (on average, 5500 cal g^{-1} dry weight) than daphniids (4500 cal g^{-1}) (Cummins, 1967). They may thus be better foods for a micropredator such as a corixid, than daphniids. Further, Wissing and Hasler (1972) indicate that daphniid caloric content decreases in early summer.

The data suggest that there is ample food available to both species in the freshwater lakes, and if C. expleta is not excluded from low salinity waters because of salinity or owing

to habitat exclusion, then it might be absent because of a need for a more special diet than C. bifida . Thus, although demonstrably not ecological homologues, the ecological preferences of C. bifida and C. expleta are still quite similar.

Miller (1967) suggested a restriction of the realised niches in sympatry may at times be the result of a competitive situation. In the two Cenocorixa species, no apparent restriction in realised niche from allopatry to sympatry was seen in terms of habitat, but there was only slight evidence of a displacement of dietary thrust in sympatry.

The present work seems to indicate little niche differentiation, a finding similar to that of Goulden (1966). However, most studies of closely related species in sympatry have detected definite differences in the ecological niches (i.e., Catchpole, 1973; Sandercock, 1967). Such differences are usually interpreted to be a result of competitive interaction, either present or in the past.

Stahl (1966) concluded that the resources in his study were essentially unlimited, and this may occur in the lakes under study. However, although food seemed to be in abundance, some effect of food quality should not be ruled out. Jansson and Scudder (1974) have suggested that food quality rather than food quantity perhaps is involved in the regulation of ovarian diapause in Cenocorixa.

The experimental results with C. bifida and C. expleta show that there is some restriction of the fundamental niche in

sympatry. However, at this time it has not been possible to conclusively demonstrate clear competition between the species, or the lack of it. The dietary requirements of the two species are extremely similar and certainly the absence of C. expleta from the freshwater lakes is not apparently owing to absence of specific food items.

Thus, although several facets of the ecology of Cenocorixa permitting the two species to coexist have been investigated, there is still no definite answer to the initial question encountered, the reasons for the exclusion of C. expleta from the most freshwater lakes. It seems likely that other, as yet undetermined, factors must be involved. The physiology of the spectes is still little understood, and may warrant further investigation. There is a need for transplantation and detailed rearing experiments. Thus in setting out to solve one problem, the present study has succeeded in elucidating some aspects of the biology of the species, but it has emphasised a need for further study of this species pair.

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