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THE ODONATA OF SOME SALINE LAKES IN BRITISH COLUMBIA, CANADA: ECOLOGICAL DISTRIBUTION AND ZOOGEOGRAPHY

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The Odonata of a series of 18 lakes on the Chilcotin Plateau of central British Columbia were examined. The lakes have similar temperature profiles, but differ widely in chemical composition and vegetation characteristics. Salinity, as measured by surface conductivity, ranges from 72 to 15524 microSiemens/cm at 25°C; the main cations are sodium and magnesium and the main anions are carbonate and bicarbonate. – Twenty-two species were found in the lake series; evidence for breeding was found for nineteen species. The distribution pattern of these species is that of a primarily freshwater group containing a few taxa that can tolerate moderate or higher salinities. No species was restricted to the higher salinity lakes. This pattern is in contrast to those of the aquatic Hemiptera and Coleoptera of the same lakes, which have very few species restricted to the fresh lakes and have some taxa restricted to the saline lakes. Cluster analysis divided the breeding fauna into three general groups: one of six common species tolerant of salinities exceeding 4000 µS/cm, one of three common species tolerant of moderate salinities (up to 1600 µS/cm), and five less common species restricted to lakes with conductivities less than 1300 µS/cm. The remaining five species had very local distributions in the fresher lakes and did not form a cluster. – The species composition reflects a predominantly northern origin of the fauna; 72% of the species have Holarctic or Boreal ranges.

INTRODUCTION

A series of saline lakes on the Chilcotin Plateau of central British Columbia presents an opportunity to examine the response of Odonata to salinity gradients. Studies of various other taxa have shown that the salinity gradient present in these lakes is important in the distribution of organisms such as aquatic angiosperms (REYNOLDS & REYNOLDS, 1975), Hirudinea (SCUDDER & MANN, 1968), Crustacea (SCUDDER, 1969a ; REYNOLDS, 1980), Corixidae (SCUDDER, 1969a, 1969b, 1983), and Chironomidae (CANNINGS & SCUDDER, 1978). The study of the odonate genus *Lestes* in these same lakes (CANNINGS *et al.*, 1980) was a more focussed segment of the observations described here.

During a wide-ranging investigation of the diversity and productivity of the littoral, profundal, and planktonic invertebrates of these lakes (LANCASTER, 1985), it was noticed that various species of Odonata were present in some lakes but not in others. Although there was no opportunity for detailed studies, the general distribution and phenology of the species present were observed from early May to mid-October, 1978.

Odonata have been cursorily mentioned in various studies of saline lakes (RAWSON & MOORE, 1944 ; BAYLY & WILLIAMS, 1966 ; SCUDDER, 1969a), but except for the *Lestes* part of the present study published previously (CANNINGS *et al.*, 1980), no examination of the way Odonata are distributed in a series of lakes of varying salinity has been undertaken. The grasslands of the Chilcotin region lie like an island in a sea of northern forests, well divorced from the warmer intermontane grasslands lying at lower elevations to the south. The bearing of this special geographic position on the composition of the dragonfly fauna was also considered worthy of investigation.

STUDY AREA

The 18 lakes encompassing a wide salinity range were selected for study from a much larger group clustered in a 25 km^2 area on Becher's Prairie near Riske Creek, British Columbia (52°00'N122°30'W) (Fig. 1). The lakes are at an elevation of 950 m and lie in depressions in a glacial till plain underlain by Permian, Triassic, and Tertiary (Miocene and Pliocene basalt) Plateau Beds (REYNOLDS & REYNOLDS, 1975 ; TOPPING & SCUDDER, 1977).

The larger lakes tend to be saline and dominated by $NaHCO_3$, the smaller ones, more properly described as ponds, are fresher, and $MgCO_3$ often prevails (CANNINGS & SCUDDER, 1978). Complete physical and chemical properties of the lakes can be found in TOPPING & SCUDDER (1977).

The climate is characterized by relatively low average annual temperatures (mean daily temperatures for January and July at Big Creek are -11.6 and 13.7°C, respectively), large fluctuations in seasonal and daily temperatures (JANSSON & SCUDDER, 1974), and low precipitation (annual mean 340.2 mm at Big Creek). The lakes are ice-covered from late October to late April.

The water bodies were chosen in order to obtain a wide range of salinities. While water chemistry varies, the use of this particular lake series kept other environmental parameters such as physical location and climate as similar as possible. In addition, the waters lack inlet and outlet streams, lack fish, and are subject to disturbance by cattle (SCUDDER, 1969a ; CANNINGS & SCUDDER, 1978).

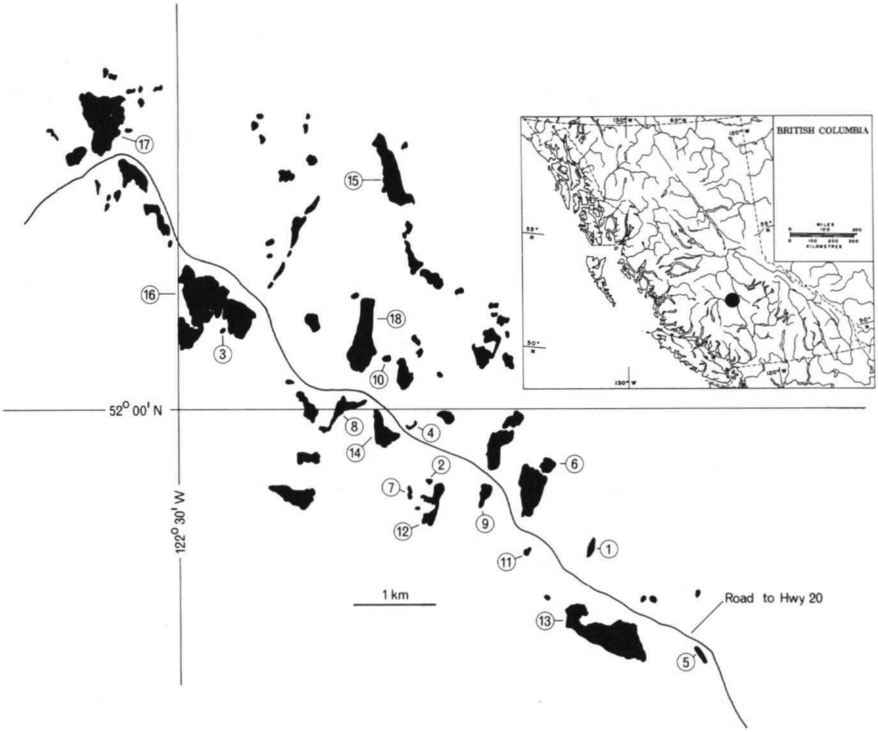

Fig. 1. The study site on Becher's Prairie, near Riske Creek, British Columbia. Inset shows the location of the area in British Columbia. The lakes are numbered according to increasing salinity as follows (lakes with unoffical, non-gazetted names are enclosed by quotation marks): (1)-"Box 27"; (2)-"Opposite Crescent"; (3)-"Centre Arms"; (4)-"Crescent"; (5)-"Near Rock"; (6)-"Near Racetrack"; (7)-"Gerrid City"; (8)-Barkley; (9)-"Box 17"; (10)-"Near Blake"; (11)-"Opposite Racetrack"; (12)-"Near Opposite Crescent"; (13)-Rock; (14)-Jackson; (15)-Long; (16)-Lye; (17)-Round-up; (18)-Barnes.

The vegetation is savanna-type upland characterized by grasses such as *Stipa richardsonii* Link, *Agropyron spicatum* (Pursh) S. & S., and *Koeleria macrantha* (Led.) J. A. Schultes, and stands of *Populus tremuloides* Minchx., *Pseudotsuga menziesii* (Mirbel) Franco, and *Pinus contorta* Douglas. In the water bodies, distinct angiosperm zonation is evident. *Zanichellia palustris* L. is usually found close inshore, with *Myriophyllum spicatum* L. and *Potamogeton* species at greater depths, and finally *Ruppia maritima* L. to a depth of 1.6 m (Reynolds & Reynolds, 1975). Marginal stands of *Juncus balticus* Willd. ring most lakes, but are stranded out of the water by midsummer. *Scirpus validus* Vahl forms isolated clumps in several lakes and *Polygonum amphibium* L. occurs in lakes with conductivities below 4000 µS/cm.

The smaller, fresher ponds are usually covered by emergent vegetation, mainly *Eleocharis palustris* (L.), *Glyceria borealis* (Nash), *Sagittaria cuneata* Sheld., and *Sparganium emersum* Rehm; some dry up by late summer. From mid-June onwards, algal blooms are common in most lakes, especially *Aphanizomenon holsaticum* Richter. In salinities above 5000 µS/cm algal blooms and submergent vegetation are virtually absent and marginal emergent vegetation is patchy; these lakes usually have relatively firm margins ringed with white salt deposits.

METHODS

Water samples were collected monthly from most of the lakes; conductivity was determined using a Radiometer CD-2 conductivity meter and the results were corrected to 25°C. Conductivities from other lakes were taken from SPENCE (1978); these represent maxima from 1975-77. Water temperatures at 1 m depth were taken from 5 May to 15 October 1978 using Ryan model-D underwater continuous chart recorders. The pH data are from CANNINGS & SCUDDER (1978); they represent the mean calculated for each lake over a number of years.

In each lake the presence or absence of larvae and adults was noted throughout the study period, and records were kept of emergence, mating, and oviposition. Larvae were collected by sweeping the littoral zone between 0 m and 1 m. Although each lake was visited several times during the summer (most every 10 days), and although the presence of every species seen was noted, we cannot assume the species list for each lake is complete. A species was considered a resident of a lake only if larvae or evidence of breeding was found.

Eighteen lakes sampled are used in the analysis; material collected at 12 additional lakes was used to augment the life-history information presented.

The unweighted pair-groups method using arithmetic averages, UPGMA, as provided by NT-SYS (ROHLF *et al.*, 1980) and recommended by SNEATH & SOKAL (1973), was used to cluster the odonates and lakes. This method follows a polythetic agglomerative hierarchical strategy clustering similar taxa or lakes together and arranging the groups into a hierarchical dendrogram. Jaccard's coefficient of similarity was used to group taxa based on their distribution, and to group lakes based on their species composition. The cophenetic correlation coefficient (SOKAL & ROHLF, 1962; ROHLF, 1974) was used to evaluate the amount of distortion associated with clusters. This technique computes the correlation between the original similarity coefficients, on which the dendrogram is based, and the cophenetic values which are a matrix of coded similarity values extracted from the dendrogram. A perfect correlation ($r = 1.00$) between the original similarity coefficients and cophenetic values indicates no distortion on converting data into a dendrogram. A correlation of $r = 0.80$ is usually considered the cut-off point for acceptable dendrograms.

RESULTS

THE ENVIRONMENT

Table I summarizes some physical and chemical parameters, including conductivities, in the lakes studied. Conductivities increased with time as the surface waters mixed with the deeper saline waters, and increases were general into September, probably owing to evaporation. The greatest changes were in lakes of high salinity. For example, the conductivity of Barnes Lake was 7629 µS/cm in May while by early September it had risen to 15524 µS/cm. Fresher lakes showed much smaller relative increases; Barkley Lake in May was 913 µS/cm and in October it was 933 µS/cm. Salinity, measured here via conductivity, therefore is a major feature of difference among the lakes.

Water temperatures rose after ice-melt in late April and reached 10°C at 1 m by the first week of May. By early June temperatures reached 20°C, and they fluctuated between about 17°C and 23°C until mid-August when they dropped below 15°C and declined steadily to 5°C by mid-October. All lakes showed a similar pattern, indicating temperature was not a factor influencing the distribution and development of species in the lakes examined.

Table I

Various physical and chemical features of the lake series

Lake	Area (ha)	Maximum Conductivity µS/cm (25°C)	pH[1]
1. Box 27	4.30	72	6.4
2. Opposite Crescent	0.23	167	
3. Centre Arms	0.59	250	
4. Crescent	0.05	370	
5. Near Rock	1.52	687	
6. Near Racetrack	1.17	748 [2]	
7. Gerrid City	0.60	970	
8. Barkley	6.32	980	8.7
9. Box 17	2.65	1070 [2]	8.6
10. Near Blake	0.64	1180 [2]	
11. Opposite Racetrack	0.90	1254	
12. Near Opposite Crescent	6.88	1568	8.6
13. Rock	34.64	3027	8.9
14. Jackson	4.55	4892	9.0
15. Long	20.66	8064 [2]	
16. Lye	46.52	9083	9.1
17. Round-up	30.84	11532	9.2
18. Barnes	17.19	15524	9.3

[1] Mean over several years.
[2] 1975-77 ; from SPENCE (1978).

DISTRIBUTION OF SPECIES

Twenty-one species of Odonata were found in the 18 study lakes (Tab. II). Larval or breeding evidence was found for 19 species ; the distribution of these is given in Table III and Figure 2. The most widespread species were *Enallagma boreale* and *Lestes congener*, which were found across the salinity spectrum and occurred in 14 and 13 lakes respectively. Thirteen of the 19 species (68.4%) were restricted to lakes with conductivities less than 1600 µS/cm. These 11 lakes had a mean of 7.2 odonate species/lake (range 2-12, SE = 1.03), whereas the 7 higher salinity lakes had a mean of only 3.0 species/lake (range 1-5, SE = 0.50). No species was restricted to the higher salinity lakes.

Cluster analysis divided the dragonflies into two groups, one of nine widespread species (the first nine species of Tab. III) and another of five less common species restricted to lakes below 1300 μS/cm in conductivity (Fig. 3). The former group is divided further into two clusters – a saline-tolerant group of six species and another of three species found in lakes with conductivities less than 1600 μS/cm. The remaining five species were each restricted to a single site and were not clustered, except for the pair *Libellula julia* and *Sympetrum obtrusum.* This dendrogram has a cophenetic correlation coefficient of 0.89, indicating relatively little distortion in converting the distribution data into a hierarchy.

Table II

Distribution of odonates in a series of saline lakes in central British Columbia. Solid circles – larval records, half-open circles – adult breeding records, open circles – adult flight records

	Box 27	Op. Crescent	Centre Arms	Crescent	Near Rock	Near Racetrack	Gerrid City	Barkley	Box 17	Near Blake	Op. Racetrack	Nr. Op. Crescent	Rock	Jackson	Long	Lye	Round-up	Barnes
Lestes congener Hagen	●	●	●		●		●	●	●		●	◐	◐	●		●		●
Lestes disjunctus Selys	●	◐	●		●		●	●	◐	●	●		○	●	●			○
Lestes dryas Kirby	●	●	●	●	●		●				●							
Coenagrion resolutum (Hagen)	●		●	○	●	◐	○	◐			●	◐				○		
Enallagma boreale Selys	●	○	●	○	●		◐	◐	◐	●	○	●	●	●	●	●	◐	●
Enallagma cyathigerum (Charp.)	●	●			○			●	●	●	●		○	○	●			○
Ischnura cervula Selys								◐				○				○		
Aeshna eremita Scudder					◐						○	○						
Aeshna interrupta Walker	●	◐			◐		●	◐						◐		●		
Aeshna juncea (Linnaeus)		●			◐						●							
Aeshna palmata Hagen		○												○				
Aeshna subarctica Walker	●				◐													
Cordulia shurtleffi Scudder																○		
Leucorrhinia borealis Hagen						◐	○				●							
Leucorrhinia hudsonica (Selys)							◐											
Libellula julia Uhler		●																
Libellula quadrimaculata L.	○																	
Sympetrum costiferum (Hagen)	●																	
Sympetrum danae (Sulzer)	●	●	●		●			◐	●	●	●		◐	●				
Sympetrum internum Mont.	●	●	○	●	●		●	◐		●	●	◐			○			○
Sympetrum madidum (Hagen)					◐									○				
Sympetrum obtrusum (Hagen)		●																

Table III

Distribution of odonates in a series of saline lakes in central British Columbia. Solid circles – larval records, half-open circles – adult breeding records

	Box 27	Op. Crescent	Centre Arms	Crescent	Near Rock	Near Racetrack	Gerrid City	Barkley	Box 17	Near Blake	Op. Racetrack	Nr. Op. Crescent	Rock	Jackson	Long	Lye	Round-up	Barnes
Lestes congener	●	●	●		●		●	●	●		●	◐	◐	●		●		●
Enallagma boreale	●		●		●		◐	◐	◐	●		●	●	●	●	●	◐	●
Aeshna interrupta	●	◐			◐		●	◐						◐		●		
Lestes disjunctus	●	◐	●		●		●	●	◐	●				●	●			
Enallagma cyathigerum	●	●						●	●	●	●				●			
Sympetrum danae	●	●	●		●			◐	●	●	●		◐	●				
Coenagrion resolutum	●		●		●	◐		◐			●	◐						
Sympetrum internum	●	●		●	●		●	◐		●	●	◐						
Lestes dryas	●	●	●	●	●		●				●							
Aeshna juncea		●			◐						●							
Leucorrhinia borealis						◐					●							
Ischnura cervula								◐										
Leucorrhinia hudsonica							◐											
Aeshna eremita					◐													
Aeshna subarctica	●				◐													
Sympetrum madidum					◐													
Libellula julia		●																
Sympetrum obtrusum		●																
Sympetrum costiferum	●																	

The lake dendrogram does not represent the data matrix as well as the odonate dendrogram – its correlation coefficient is 0.80, indicating a marginal fit. Basically, the lakes are divided into two main groups – one containing nine of the less saline lakes (<1300 μS/cm) and another containing six of the higher salinity lakes. Long Lake, which is considered saline (8064 μS/cm), is grouped with the nine low salinity lakes. "Crescent" and "Near Racetrack" were not clustered.

SPECIES PHENOLOGY

Lestes congener Hagen – Adults appeared on 6 July at Barnes Lake but did not emerge from any other lake until 23 July. By 27 July the last emergence had apparently occurred. Adults were still abundant, actively copulating and ovipositing on 14 October.

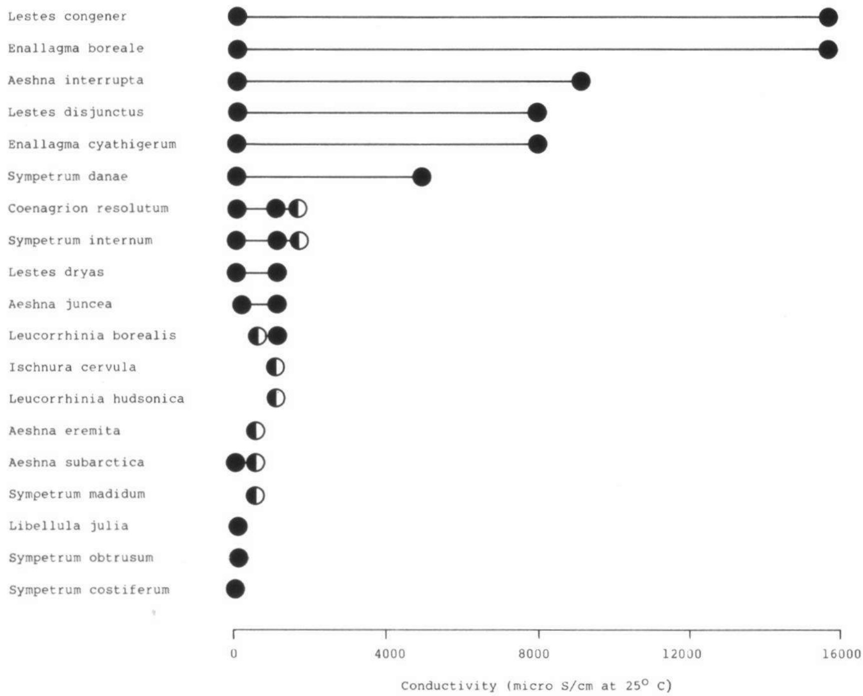

Fig. 2. Distribution of Odonata with regard to salinity in the Becher's Prairie lake series. Solid circles – larval records, half-open circles – adult breeding records.

Lestes disjunctus Selys – Adults first emerged on 27 June in "Box 27". Most of the emergence took place in the first week of July ; 6 July (Barkley) is the latest date. Copulation and oviposition were first noted on 9 July, but most occurred in the last week of the month. Adults were last seen on 4 August.

Lestes dryas Kirby – Adults emerged from 16 June ("Near Rock") to 27 June ("Centre Arms"). Mature adults were observed from 26 June to 26 July.

Coenagrion resolutum (Hagen) – Emergence occurred from 16 May ("Opposite Race-track") to 27 June ("Centre Arms") and probably peaked around 1 June. Copulating adults were seen from 3 June ("Box 27") to 6 July (Barkley). Adults were seen as late as 23 July ("Near Rock"), but they had already disappeared from other ponds ("Opposite Crescent", "Near Opposite Crescent") by this time.

Enallagma boreale Selys – The first adult was seen on 18 May (Lye), but most emerged in late May and early June ; the latest emergence was noted on 6 July (Jackson). Copulation and oviposition were observed from 3 June ("Box 27", Rock) to 27 August (Lye) ; the last adult was seen on 13 September (Rock).

Enallagma cyathigerum (Charpentier) – A large emergence occurred at "Box 27" on 3 June ; some were still emerging there on 15 June. Mating was observed from 7 June ("Kettlehole", "Near Pothole") to 14 July ("Junction Range") ; the last adult was recorded on 23 July ("Near Rock"). Large larvae were found on 25 July ("Box 17") and 26 July ("Centre Arms").

Ischnura cervula Selys – Adults were first found at Lye on 7 June and were subsequently seen on 6 July (Barkley – copulation) and 9 July (Rock).

Aeshna eremita Scudder – Adults were recorded from 21 July ("Slash") to 14 October ("Near Opposite Crescent"); mating was noted on 21 July and 23 July ("Near Rock").

Aeshna interrupta Walker – Emergence was recorded only on 15 June ("Box 27"); in 1977 large larvae were found on 28 June ("Gerrid City"). Copulation and oviposition were noted from 6 July (Jackson) to 27 August ("Opposite Crescent"). The latter date is the last flight record.

Aeshna juncea (Linnaeus) – Adults were caught only on 23 July ("Near Rock" – ovipositing, "Opposite Crescent" – mating).

Aeshna palmata Hagen – There were two records of adults – 23 July ("Opposite Crescent") and 14 October (Jackson).

Aeshna subarctica Walker – One record of adults – a mating pair and a female at "Near Rock" on 23 July.

Cordulia shurtleffi Scudder – An adult female was caught at Lye on 7 June.

Leucorrhinia borealis Hagen – Teneral adults were at "Gerrid City" on 26 May and copulation was observed on 5 June ("Near Racetrack"). The latest flight record was 25 June ("Near Opposite Racetrack").

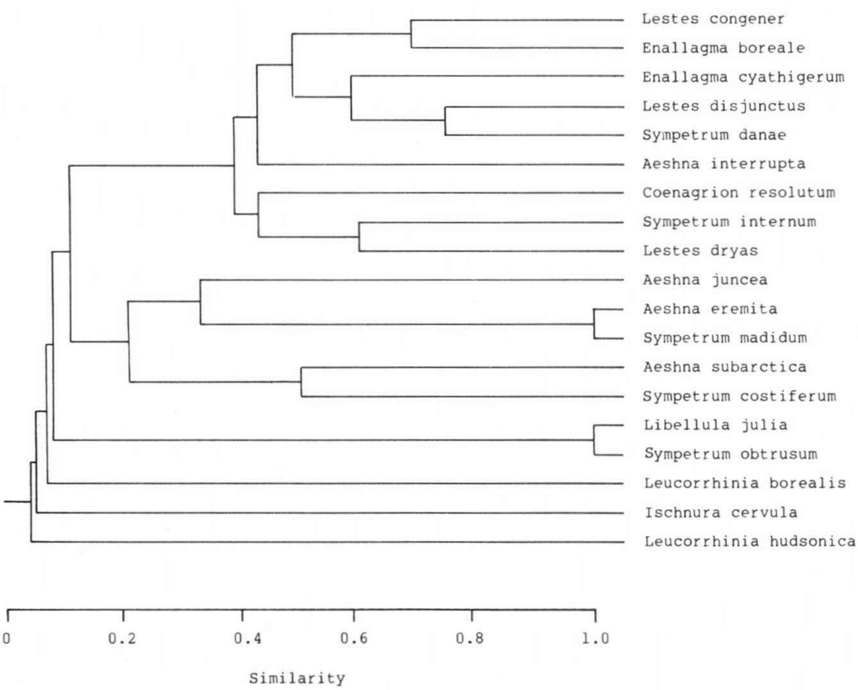

Fig. 3. Dendrogram of odonates clustered on the basis of presence/absence distribution in the lakes; r = 0.89.

Leucorrhinia hudsonica (Selys) – Mating adults were seen from 26 May ("Gerrid City") to 28 June ("Dam").

Libellula julia Uhler – One larval record only – three overwintering larvae on 27 August ("Opposite Crescent").

Libellula quadrimaculata Linnaeus – A "day-old teneral" was caught at "Box 27" on 3 June. Mating and oviposition were noted on 28 June ("Dam").

Sympetrum costiferum (Hagen) – Exuviae were found 23 July ("Near Opposite Racetrack") and teneral adults 4 August ("Box 27"). Mating and oviposition were noted at "Box 27" on 4 August and 23 September.

Sympetrum danae (Sulzer) – Adults first appeared 14 July ("Junction Range") and were still emerging on 25 July ("Box 17", "Box 27"). Copulation and oviposition were recorded from 25 July ("Box 17") to 23 September ("Box 27").

Sympetrum internum Montgomery – Tenerals were found on 25 June ("Opposite Racetrack") and emergence continued until at least 25 July ("Box 27"). Mating and oviposition were observed from 6 July (Barkley) to 27 August ("Opposite Crescent"); the latest flight record was 3 September ("Box 27").

Sympetrum madidum (Hagen) – Teneral adults first appeared on 2 June (Jackson) and adults were last seen on 23 July ("Near Rock" – copulating).

Sympetrum obtrusum (Hagen) – One larval record only – 23 July ("Box 27").

DISCUSSION

LOCAL DISTRIBUTION

In general, the odonate distribution pattern in the Becher's Prairie lake series is that of a primarily freshwater group containing a few taxa that can tolerate moderate or higher salinities. This pattern is in contrast to those of the Hemiptera and Coleoptera in the same lakes. Only 1 of 8 aquatic Hemiptera (12.5%) and 8 of 28 (28.6%) aquatic Coleoptera species are restricted to lakes with conductivities less than 1600 µS/cm (LANCASTER, 1985) compared to 68.4% of the Odonata. In addition, 2 of 8 (25%) aquatic Hemiptera and 5 of 28 (17.9%) aquatic Coleoptera species are restricted to saline lakes (> 4000 µS/cmS/cm) (LANCASTER, 1985), whereas no odonate species was.

Previous studies on this lake series (SCUDDER, 1969a; REYNOLDS & REYNOLDS, 1975, CANNINGS & SCUDDER, 1978; LANCASTER, 1985) show a distinct difference between the biota of lakes with conductivities over about 4000 µS/cm and those of fresher lakes. Lakes above 4000 µS/cm correspond to those designated by WILLIAMS (1966) as saline; that is, lakes with dissolved solids greater than 3000 ppm. In past studies, saline lakes were represented by Lye, Round-up, and Barnes Lakes (Long Lake has not been studied previously), but the overall salinity of the lake series seems to be increasing so that, in 1978 at least, Lake Jackson (4892 µS/cm) would be considered saline. The dragonfly fauna of these saline lakes is simply a subset of the common, widespread species of the area. Although this fauna is separated from the rest of the local fauna in a secondary dichotomy of the odonate dendrogram (Fig. 3), the main dichotomy is between common species living in lakes with conductivities of at least 1254 µS/cm and less common species restricted to fresher lakes (≤ 1254 µS/cm). The main dichotomy of the lake dendrogram (Fig. 4) also divides the lakes between conductivities of 1254 and 1568 µS/cm.

The clustering of Long Lake with the much less saline "Box 17" and "Near Blake" is explained by the presence of both *Enallagma* species in Long Lake (*E. cyathigerum* is at its upper salinity limit there), by the absence of the widespread *Lestes congener* from both Long and "Near Blake", and by the relatively depauperate fauna of the two fresher lakes. Although *Enallagma cyathigerum* larvae were found in Long Lake, all 50 adult *Enallagma* caught there were *E. boreale.*

Since submerged vegetation plays an important part in the existence of many Odonata larvae, the fauna of these lakes may be limited by water chemistry both directly, through salinity tolerance, and indirectly, through its effect on plant distribution. REYNOLDS & REYNOLDS (1975) found that lakes with salinities greater than those of Lake Jackson contained no submerged

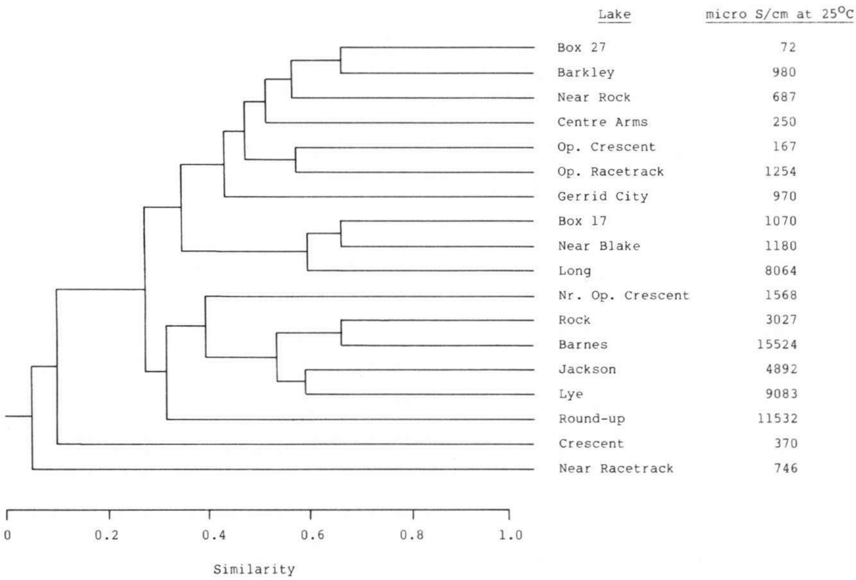

Fig. 4. Dendrogram of lakes clustered on the basis of their odonate fauna ; r = 0.80.

plants. Most odonate species of the lake series, however, drop out of the salinity gradient at conductivities below that of Lake Jackson, a water body normally rich in aquatic vegetation.

Certain plants may also be missing from lakes within their salinity range, possibly for edaphic reasons, and hence influence the distribution of dragonflies. CANNINGS *et al.* (1980) state that the absence of *Juncus balticus* from Round-up Lake may explain the corresponding absence of *Lestes congener.* The lack of emergent vegetation along the shores of Rock and "Near Opposite Crescent" Lakes may be the cause of the depauperate fauna recorded there. CANNINGS *et al.* (1980) suggest that *Lestes congener* and *L. disjunctus* are absent from these lakes because there are no emergent plants in which to lay eggs.

LANCASTER (1985) clustered eight of the lakes ("Box 27", Barkley, "Near Opposite Crescent", Rock, Jackson, Lye, Round-up, and Barnes) using species distribution and relative abundance of aquatic vegetation. The resulting dendrogram (not figured here) matches in many ways the one based on dragonfly distribution (Fig. 4). In the floral dendrogram, "Box 27" and Barkley are separated from the more saline lakes, although they are not paired, and "Near Opposite Crescent" is clustered with the more saline lakes but is separated from the main cluster and placed near the fresh lakes. The main difference between the two figures is that the dendrogram based on odonates separates Round-up from the other saline lakes (since it has only one odonate, *Enallagma boreale*) whereas Rock is separated from the others on the basis of vegetation (because of a great abundance of submergents).

Other factors, such as the degree of permanence of lakes, also affect the local distribution of dragonflies. "Crescent" is separated from the other lakes (Fig. 4) because its early drying up (mid-July in 1978) eliminates odonates that develop as larvae through the late summer (e.g. *Enallagma, Coenagrion*) or ones that do not emerge until late July or August (*Lestes congener* and perhaps *Sympetrum costiferum, S. danae,* and *S. obtrusum*). "Centre Arms" also dried up, but not until mid-August, giving species such as *Lestes congener* and *Sympetrum danae* time to complete development. "Near Racetrack" is not clustered because of its depauperate, freshwater fauna, possibly a result of insufficient collecting.

The distribution of *Sympetrum costiferum* on Becher's Prairie is worthy of mention. WALKER & CORBET (1975) state that this species "appears to be the *Sympetrum* that is most tolerant of saline waters", although our studies show it to be restricted to the very freshest lake of the series.

ZOOGEOGRAPHY

The following discussion divides the species list into several elements reflecting the distribution patterns of the taxa.

Holarctic (27%). – Six of the 22 species are circumboreal and most have distributions that range far to the south – *Lestes dryas* to Oklahoma and California, *Enallagma cyathigerum* to Nevada and California, *Libellula quadrimaculata* to Texas and *Sympetrum danae* to California. *Aeshna juncea* and *Aeshna subarctica* are northern and montane in North America, occurring mostly in Canada.

Boreal (45%). – The largest component of the fauna, these species occur transcontinentally mainly in the boreal coniferous forests of Canada and the northern United States. Indeed, if Holarctic species are included here, as they are inhabitants of the same life zones, this northern element would make up 72% of the species. The mountains of the Cordillera allow some boreal species access far to the south ; *Aeshna eremita*, for example, ranges to Utah. Other species in this category are *Lestes congener* and *L. disjunctus, Coenagrion resolutum, Enallagma boreale, Aeshna interrupta, Cordulia shurtleffi, Leucorrhinia borealis, L. hudsonica*, and *Libellula julia*. *Leucorrhinia borealis* does not range transcontinentally, but its wide distribution in northern forests west of Hudson's Bay and in the Cordillera places it in the Boreal category.

Southern (13%). – *Sympetrum costiferum, S. internum*, and *S. obtrusum* occupy predominantly southern and central transcontinental ranges. They have, to a large extent, penetrated into higher elevations and latitudes.

Western (10%). – *Ischnura cervula* and *Sympetrum madidum* are found mainly at low elevations in western valleys and are not recorded much farther north than the study area in British Columbia.

Cordilleran (5%). – *Aeshna palmata* is a species of western montane origin.

Becher's Prairie is one of the most northerly outliers of the intermontane grasslands of western North America. However, because it is situated on a mainly forested plateau separated from the warmer grasslands of the valleys of southern British Columbia, the character of its odonate fauna is more similar to that of the aspen parkland at the southern edge of the boreal forest on the Canadian Great Plains (where species such as *Enallagma boreale, Coenagrion resolutum, Aeshna interrupta*, and *Leucorrhinia borealis* are dominant) than it is to the grasslands of the valleys to the south, which are influenced by Western and Southern faunas. Except for *Ischnura cervula*, the few southern elements that populate this plateau mostly are species that have penetrated the northern forests for considerable distances. *Sympetrum internum* ranges north to the central Yukon, and *S. costiferum* and *S. obtrusum* are known as far north as Great Slave Lake, Northwest Territories. *S. madidum* reaches even farther north to Norman Wells in the relatively low and warm (for the Boreal forest) Mackenzie River Valley; in British Columbia, however, Becher's Prairie is the most northerly recorded locality. *Ischnura cervula* is very rare at this altitude and latitude, although it has been captured at two localities to the north.

PHENOLOGY

Lestes spp. — CANNINGS *et al.* (1980) point out that the staggering of development periods of the three species of *Lestes*, where they coexist, may reduce interspecific competition between similar-sized larval instars as well as between adults. Indeed, *L. congener* emerged 17 days earlier in Barnes Lake (where it is the only *Lestes* present) than in any other lake, and its emergence period there was twice as long as in any other lake, indicating that its possible emergence period is much broader than its actual one in sympatric lakes.

Coenagrion resolutum — The flight period of *Coenagrion resolutum* on Becher's Prairie is approximately the same as its flight period at similar latitudes in Alberta (WALKER, 1953); this is earlier and shorter than the dates given by CANNINGS & STUART (1977) for other British Columbia sites.

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