Odonatologica 9 (1): 19-28 *March 1, 1980*

THE DISTRIBUTION OF THE GENUS *LESTES* IN A SALINE LAKE SERIES IN CENTRAL BRITISH COLUMBIA, CANADA (ZYGOPTERA: LESTIDAE)

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Received November 5, 1979

L. congener Hag., *L. disjunctus* Sel. and *L. dryas* Kirby were found to be common inhabitants of a saline lake series on the Chilcotin Plateau of central British Columbia. *L. unguiculatus* Hag., the only other sp. of the genus in British Columbia, did not occur in the region, although it is characteristic of similar habitats at lower elevations 130 km to the south. — In the lakes studied, ionic concentrations and compositions differed considerably. Conductivities ranged from 72 to 15524 micromhos/cm at 25°C; the main cations were sodium and magnesium and the main anions were carbonate and bicarbonate. — *L. dryas* colonized only the fresher water bodies, those with conductivities up to 1254 micromhos/cm and pH levels below 9.0, while *L. disjunctus* occurred in lakes with conductivities up to 4892 micromhos/cm and pH measurements to 9.0. *L. congener* inhabited the complete range of salinities examined and occurred in very large numbers even at the upper limit of conductivity and at a pH of 9.3. — Emergence and mating of the 3 spp. were temporally separate; *dryas* emerged 10 or 11 days before *disjunctus*, which preceded *congener* by 9 days. The main *disjunctus* emergence occurred approximately 20 days before the peak of the *congener* emergence. — The possible influences of salinity on both the distribution of the species within the lake series and the timing of their emergence were examined.

INTRODUCTION

Studies have been undertaken on the flora and fauna of a series of saline lakes in the Chilcotin region of central British Columbia on the assumption that the environmental gradients characteristic of these lakes would result in distinctive distribution patterns. In several cases it has been established that the salinity gradient is important in the distribution of organisms in these lakes, for example, aquatic angiosperms (REYNOLDS & REYNOLDS, 1975), Hirudinea (SCUDDER & MANN, 1968), Crustacea (SCUDDER, 1969), Corixidae (SCUDDER, 1969) and Chironomidae (CANNINGS & SCUDDER, 1978).

During an investigation of the littoral, profundal and planktonic invertebrates of these lakes it was noted that the larvae of three species of the genus *Lestes* (Odonata: Lestidae) were present in some lakes but not in others. Despite the lack of opportunity for a detailed study, the distribution and gross phenology of the species were observed from early May to mid-October, 1978. Three species, *L. congener* Hagen, *L. disjunctus* Selys and *L. dryas* Kirby occurred in the lakes, although the fourth species found in British Columbia, *L. unguiculatus* Hagen, did not.

Although the life cycles of these species have been studied in considerable detail elsewhere (GARDNER, 1952; INGRAM, 1976), especially in Saskatchewan (SAWCHYN & CHURCH, 1973; SAWCHYN & GILLOTT, 1974a, 1974b), and although Odonata have been mentioned in saline lake studies (RAWSON & MOORE, 1944; BAYLY & WILLIAMS, 1966), as far as we know, no examination of the way Odonata are distributed in a saline gradient has been published. This study is not a thorough examination of the problem, but is rather a preliminary investigation designed to indicate some promising directions for future research.

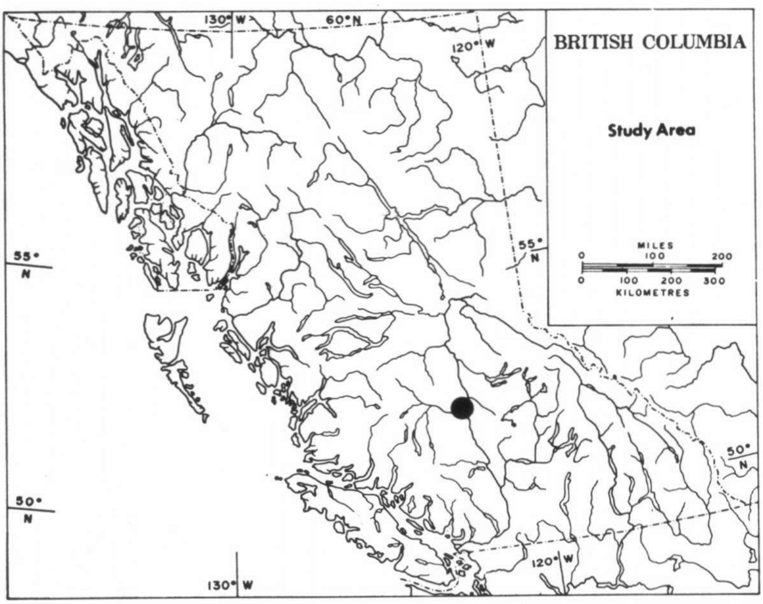

Fig. 1. Location of the study area.

STUDY AREA

The 14 lakes examined are situated on Becher's Prairie near Riske Creek, British Columbia (Fig. 1). The lakes are in depressions in glacial till underlain by Permian, Triassic and Tertiary Plateau beds (REYNOLDS & REYNOLDS, 1975). Mean precipitation is 35 cm annually and mean daily temperatures for January and July are -11.6°C and 13.7°C respectively. The lakes are ice-covered from mid-October to late April (CANNINGS & SCUDDER, 1978).

The lakes vary in both size and character; the larger, more saline ones are generally dominated by $NaHCO_3$ while in the smaller, fresher lakes, $MgCO_3$ often prevails (CANNINGS & SCUDDER, 1978). Detailed physical and chemical properties of the lakes are given in TOPPING & SCUDDER (1977).

Some of the more common Odonata (aside from the *Lestes* species) inhabiting the lake series include *Coenagrion resolutum* (Hagen), *Enallagma boreale* Selys, *E. cyathigerum* (Charpentier), *Aeshna interrupta* Walker, *Leucorrhinia borealis* Hagen, *Sympetrum danae* (Sulzer) and *S. internum* Montgomery.

METHODS

Water samples were collected monthly and conductivity determined using a Copenhagen radiometer; results were corrected to 25°C. Water temperatures at the 1m depth were measured from 5 May to 15 October using Ryan underwater continuous chart recorders. The pH data used are from CANNINGS & SCUDDER (1978) and represent the mean reading calculated for each lake over a number of years.

In each lake the presence or absence of larvae and adults of each species of *Lestes* 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 with a net. Larvae and adults were preserved in 70 per cent ethanol.

RESULTS

ENVIRONMENT

Table I summarizes the conductivity range in the lakes studied; the measurements given are the highest levels recorded for the period. Conductivities increased as the surface waters became mixed with the more saline waters beneath, and increases were general into September, probably owing to evaporation. The greatest changes were in the more saline lakes; for example, the conductivity of Barnes Lake in May was 7629 micromhos/cm, while in early September it was 15524 micromhos/cm. Fresher lakes showed much smaller relative increases in conductivity; Barkley Lake increased from 913 micromhos/cm in May to 933 micromhos/cm in October. Salinity, measured here via conductivity, is thus a major difference among the lakes.

Water temperatures rose rapidly after the ice melted in late April and reached 10°C at 1 m in the first few days of May. By early June 20°C had been reached, and temperatures fluctuated between about 3°C above and below this figure until mid-August when they dropped below 15°C and declined steadily to about 5°C by mid-October. Patterns in all lakes were similar, suggesting that temperature was not a factor influencing the differences in distribution and development of the Odonata in the lakes studied.

DISTRIBUTION OF *LESTES* SPECIES

The distribution of *Lestes congener*, *L. disjunctus* and *L. dryas* with respect to the salinity gradient is shown in Table I. A species was considered present in a lake only if larval development occurred there; observations of copulation or oviposition were not considered valid criteria for determining distribution. Even so, no species was seen copulating or ovipositing at lakes with greater conductivities than those in which that species was known to develop.

L. dryas colonized only the fresher water bodies, those with conductivities up to 1254 micromhos/cm and pH levels below 9.0. These are small, shallow ponds completely covered with emergent vegetation (mainly *Eleocharis*

Table I

Distribution of *Lestes* species in a series of saline lakes in central British Columbia.

Lake	Highest conductivity µmhos/cm (25°C)	pH*	*dryas*	*disjunctus*	*congener*
"Box 27"	72	6.4	●	●	●
"Opposite Crescent"	167	—	●		●
"Centre Arms"	250	—	●	●	●
"Crescent"	370	—	●		
"Near Rock"	687	—	●	●	●
"Gerrid City"	970	—	●	●	●
Barkley	980	8.7		●	●
"Opposite Racetrack"	1254	—	●	●	●
"Nr. Opp. Crescent"	1568	8.6			
Rock	3027	8.9			
Jackson	4892	9.0		●	●
Lye	9083	9.1			●
Round-up	11532	9.2			
Barnes	15524	9.3			●

* Mean over several years.

palustris (L.), *Glyceria borealis* (Nash), *Sagittaria cuneata* Sheld., *Sparganium emersum* Rehmann and *Potamogeton natans* L.) and tend to dry up in the summer. *L. dryas* was absent from Barkley Lake, a lake within its salinity tolerance, but one which is deeper, has emergent vegetation only around the shore, and does not dry up.

L. disjunctus occurred in lakes with conductivities up to 4892 micromhos/cm and pH measurements to 9.0.

L. congener inhabited the complete range of salinities examined and occurred in very large numbers even in Barnes Lake which reached a high conductivity of 15524 micromhos/cm in September and had a mean pH of 9.3. Round-up Lake had no *Lestes* present (although one might expect to find *L. congener* there), probably the result of a complete lack of emergent vegetation in the areas sampled.

PHENOLOGY OF *LESTES* SPECIES

The temporal pattern of emergence and adult activity of the three species in the lake series is shown in Figure 2.

L. dryas was the first of the three species to emerge in the spring. It appeared in "Near Rock" pond on 16 June and was last seen emerging on 27 June in "Centre Arms" pond. Mature adults were first observed on 26 June and none were seen after 26 July.

L. disjunctus first emerged on 27 June in "Box 27" pond. Most of the emergence in the lakes as a whole took place in the first week of July; 6 July (Barkley Lake) is the latest date. Copulation and oviposition were first noted on 9 July, but most occurred in the last week of that month. The species was last seen on 4 August.

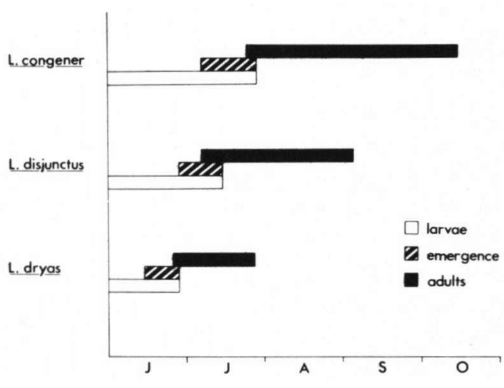

Fig. 2. Emergence and flight period of *Lestes* species in the lake series as a whole.

Adults of *L. congener* appeared on 6 July at Barnes Lake but did not emerge from any other lake until 23 July. By 27 July the last emergence apparently had occurred. Adults were still abundant at several lakes and were actively copulating and ovipositing on 14 October, the last date observations were made. During the last week of the study ice was present along the lakeshores in the morning.

In the fresher lakes emergence of the species, where they coexisted, generally followed the pattern outlined above for the lake series as a whole (Fig. 2). The emergence timing and pattern in Barnes Lake (Fig. 2) is worthy of mention. In this, the most saline lake studied, *L. congener* was the only *Lestes* species present. It emerged 17 days earlier here than in any other lake, and the emergence period lasted 21 days, at least twice as long as in the other lakes.

The drying of water bodies may affect the presence or absence of species in that body. "Crescent" pond dried up early in the summer; it was dry on 19 July (Fig. 2) but probably was dry by at least 15 July. Only *L. dryas* developed in this pond in 1978. "Centre Arms" pond was dry by 17 August (Fig. 2) but all three species developed here.

In general, *L. dryas* emerged about 10 or 11 days before *disjunctus*, which preceded *congener* by 9 days. The main *disjunctus* emergence occurred approximately 20 days before the peak of the *congener* emergence.

DISCUSSION

Previous studies on the lake series in question (SCUDDER, 1969; REYNOLDS & REYNOLDS, 1975; CANNINGS & SCUDDER, 1978) show a sharp division between the flora and fauna found in the lakes with conductivities over about 4000 micromhos/cm and those of fresher lakes. Such conductivities are found in lakes saltier than Lake Jackson (REYNOLDS & REYNOLDS, 1975; CANNINGS & SCUDDER, 1978). These lakes correspond to those designated by WILLIAMS (1966) as saline; that is, lakes with dissolved solids greater than 3000 ppm. Moreover, these lakes (Lye, Round-up, Barnes) were found to be closely related and distinct from the fresher lakes when classified statistically using complete physicochemical data (TOPPING & SCUDDER, 1977). In this case, the question of whether chemical concentration or composition is more important was avoided by considering both equally and simultaneously (TOPPING & SCUDDER, 1977).

Our results indicate *congener* to be the only *Lestes* species studied that can develop in the most saline waters above 5000 micromhos/cm. Indeed, here it is very abundant, and except for *Enallagma boreale*, is the only zygopteran to occur. In these high salinity lakes the adults oviposit in, and the larvae live among, the stems of *Juncus balticus* Willd., one of the few emergent plants that occur in these situations. In lakes, with relatively high conductivities where such vegetation is absent, possibly because of shoreline structure (e.g. Round-up Lake), *L. congener* is absent.

The absence of *Lestes* species in "Near Opposite Crescent" and Rock Lakes which from a salinity and submerged vegetation standpoint appear habitable for at least *disjunctus* and *congener*, may be owing to a lack of suitable oviposition sites. Emergent vegetation was absent from the shoreline, presumably because of edaphic factors.

REYNOLDS & REYNOLDS (1975) found that lakes in this same series having conductivities higher than that of Lake Jackson contained no submerged plants. Since submerged vegetation plays an important part in the existence of many Odonata larvae, the dragonfly fauna of these lakes may be limited by water chemistry both directly, through salinity tolerance, and indirectly, through the effet on plant distribution (REYNOLDS & REYNOLDS, 1975). Such may be the case with *L. disjunctus*, which is not found in lakes without dense submerged vegetation. In medium salinities, that is, in those lakes with conductivities above about 1000 micromhos/cm near the upper limit of *L. dryas* distribution, this vegetation is mainly *Myriophyllum spicatum* L. *L. dryas* was found only in water bodies with dense emergent vegetation. It was restricted to very shallow ponds with conductivities below about 1200 micromhos/cm that usually dry up in the summer. WALKER (1953) considered it a species of temporary water bodies.

In general, emergence dates of the three species are similar to those reported for the same species in Saskatchewan by SAWCHYN & GILLOTT (1974a, 1974b), and it is likely their development is similar in the two localities. The climate is rather similar in both places, with perhaps colder winters in Saskatchewan. Although *L. unguiculatus* is considered a southern species in British Columbia (CANNINGS & STUART, 1977), its absence in these saline lakes is interesting, for SAWCHYN & GILLOTT (1974b) found the eggs as cold hardy as those of *L. disjunctus* in Saskatchewan. *L. unguiculatus* is a common and characteristic inhabitant of alkaline ponds in the hotter regions only 130 km to the south in British Columbia.

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. Certainly breeding adults of *dryas* and *congener* are completely temporally segregated (Figs. 2, 3), and *disjunctus* adults are similarly separated from those of the other two species at least during the height of their breeding periods. A similar situation exists in the life cycles of *Ischnura* (Coenagrionidae) species in southwestern British Columbia (CANNINGS & DOERKSEN, 1979). In the same lakes under study CANNINGS & SCUDDER (1979) found three species of *Chironomus* (Diptera) to exhibit emergence chronologies similar to those of these *Lestes* species. Some temporal reproductive isolation between the three species was suggested.

The eggs of *L. congener* enter diapause and overwinter at an early stage of embryonic development while those of *dryas* and *disjunctus* overwinter at the end of this development (SAWCHYN & CHURCH, 1973). For all species the wetting of the egg in spring when the ice melts initiates post-diapause development (SAWCHYN & GILLOTT, 1974b). Although the larvae of *congener* develop very rapidly, the amount of embryonic development necessary in the spring results in a late hatching date (late May in Saskatchewan) and accounts for the late appearance of the adults (SAWCHYN & GILLOTT, 1974a).

Since *L. congener* is known to oviposit in standing dead stems (SAWCHYN & GILLOTT, 1974a, 1974b) (it uses the dried stems of *Juncus balticus* and *Eleocharis palustris* in the Chilcotin study area), it can colonize ponds in summer even if the emergent vegetation is dead. Of course, the species is restricted to those ponds that do not dry up until after late July when the adults emerge. Thus, *L. congener* did not emerge from "Crescent" pond which dried up by 19 July, and no adults were seen ovipositing in the dried vegetation. Presumably no eggs were laid in this basin in 1977 either, for no *congener* larvae were found here while water was present. However, *congener* was able to complete development in "Centre Arms" pond, which did not dry up until mid-August. Depending on the amount of water present in each basin, and depending on how quickly this water evaporates, the distribution of the three species, but especially of *congener*, may change from year to year in the lakes.

The absence of *L. disjunctus* from "Crescent" pond cannot be explained by a lack of water in late July since this species emerges before mid-July. SAWCHYN & GILLOTT (1974b) state that both *disjunctus* and *dryas* must lay eggs in green, moist stems for the pre-diapause development to occur before the winter begins. In 1977, which was a drier year than 1978, "Crescent" pond probably dried in the first half of July and the eggs of *disjunctus*, if any were laid, perhaps were not able to develop in the rapidly drying stems. *L. dryas*, with its early emergence and

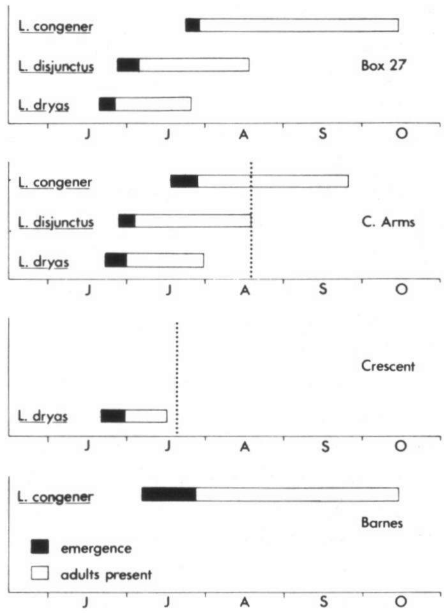

Fig. 3. Emergence and flight period of *Lestes* species in selected water bodies. Vertical dotted lines indicate the date the water body dried up.

early oviposition time, would be able to colonize ponds that dried up very early, since pre-diapause development of the egg could be completed before the stems died (SAWCHYN & GILLOTT, 1974b).

Compared with first emergence times of *L. congener* in Saskatchewan (21 July 1970) (SAWCHYN & GILLOTT, 1974a) and in the fresher lakes in this study (23 July), the species' very early emergence in Barnes Lake poses interesting questions. In this lake, the most saline and basic studied, the conductivity reached 13214 micromhos/cm by early July, 14852 micromhos/cm by 4 August and 15524 micromhos/cm by 4 September. Apparently the larval development of *L. congener* is shortened in this lake by about 17 days, judging by the emergence period in nearly, fresher lakes. Shortened larval life was noted in some Odonata living in Australian saline lakes (BAYLY & WILLIAMS, 1966). Given the great increase in the salinity of Barnes Lake over the summer it is possible such rapid development is an adaptation of the population in this lake that permits completion of larval life while salinities are tolerable (BAYLY & WILLIAMS, 1966). It is also possible that the lack of other *Lestes* species in this lake, and the lack of constraints due to competition results in a loss of synchrony in the emergence period of the species relative to the emergence pattern in lakes where congeneric species occur. The relatively long emergence period of *congener* in Barnes Lake, 21 days as compared to six to ten days in other lakes, alsy may reflect a lack of competition. It is significant that similar asynchrony in the emergence pattern of *Chironomus athalassicus* Cannings (Diptera: Chironomidae) was found in Barnes Lake where the species was without close relatives compared with highly synchronous emergence in lakes where sympatric congeneric species occurred (CANNINGS & SCUDDER, 1979).

In conclusion, it may be noted that *Lestes* species have distinct and different distribution patterns in the saline lakes studied. This is likely a result both of the direct influence of water chemistry (the total concentration of ions, the concentration of individual ions, etc.) and of the distribution of various aquatic plants. The time of drying up of some water bodies also may affect distribution. The change in the emergence pattern of *L. congener* in the most saline lakes may be an adaptation to existence in high solute concentrations or perhaps to biotic factors as yet not elucidated. The study is of a speculative nature and produces more questions than it answers, but indicates such a saline lake series offers fertile ground for further research on the Odonata in general and the genus *Lestes* in particular.

ACKNOWLEDGEMENTS

The research for this paper was supported by a grant to Dr. G.G.E. SCUDDER from the National Research Council of Canada. Dr. Scudder criticized the manuscript.

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