

Life History of *Sialis* (Megaloptera: Sialidae) in a Lentic and Lotic Ecosystem in Central Texas

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ABSTRACT.—We studied the life history and feeding habits of two coexisting and closely related sister species of *Sialis* (*Sialis itasca* Ross and *Sialis velata* Ross) from a reservoir and river in central Texas. Measurement of larval head capsules and emergence showed the two species to have 10 larval instars, and the seasonal distribution of immature and adult life stages showed synchronous, seasonal, univoltine life histories with a single cohort. Life history dynamics were somewhat faster in the river, probably due to higher temperatures during the larval growth periods. Larvae exhibited a more rapid larval development rate and earlier prepupal and adult emergence patterns relative to those reported from more northern latitudes. However, a univoltine life cycle appears to represent the norm for *Sialis* in geographic locations where water temperatures are not limiting to growth and suggests that evolutionary/genetic constraints play a greater role in regulating life history in these insects than environmental factors. Analysis of larval diets showed prey consumed by members of both populations consisted of ostracods, oligochaetes and chironomids.

INTRODUCTION

Life history information is important in understanding structural and functional roles of macroinvertebrates in aquatic environments since they constitute a major component of the biomass and secondary productivity in both lentic and lotic ecosystems (Brittain, 1990). Specifically, life history is used as a basis for secondary production estimates (Huryn and Wallace, 2000), environmental impact assessments (Smock, 1988) and in ecological experiments such as predator-prey or competition studies (Azam and Anderson, 1969). Also, variation in life histories of aquatic insects may be a potential indicator and predictor of changes in environmental temperatures associated with anthropogenic activities such as river regulation, reservoir construction, thermal discharge, deforestation and changes in land use (Elliot, 1996). Life history patterns among closely related species are generally similar, but phenology and voltinism can vary in different ecosystems with different environmental conditions (Butler, 1984; Smock, 1988). Environmental factors, such as temperature, food quantity and quality and photoperiod, are thought to be responsible for most life history variations found in closely-related species (Sweeney, 1984; Hayahsi, 1988, 1996; Elliot, 1996; Sweeney *et al.*, 1992; Giller and Malmqvist, 1998). As a result, geographical

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location is an important consideration when evaluating life histories for organisms having wide distributional patterns. For some species occurring at northern latitudes of North America where summers are short, fewer generations are produced per year compared with those occurring in southern latitudes (Corbet, 1980; Ward and Stanford, 1982; Giller and Malmqvist, 1998). For example, Short *et al.* (1987) found the megalopteran, *Corydalus cornutus*, to produce a generation in as little as 6 mo in central Texas, while Knight and Simmons (1975) reported development taking 3 to 4 y in Michigan. Similarly, Bowles (1990) found *C. cornutus* to have univoltine life histories at southern latitudes, but suggested that longer life histories are likely at more northern latitudes. In addition, life history variation can also occur locally in streams or rivers with different temperature regimes (Short *et al.*, 1987; Hayashi, 1996).

The Sialidae are distributed worldwide (Hayashi, 1997) with 23 known species in North America (Ross, 1937; Whiting, 1991a, b; Flint, 1964; Townsend, 1939). Life history studies have been completed for several species of *Sialis* in northern temperate regions of North America and Europe including *S. rotunda* (Azam and Anderson, 1969), *S. lutaria* (Giani and Laville, 1973; Brooker, 1979; Iverson and Thorup, 1987; Elliot, 1996), *S. cornuta* (Pritchard and Leischner, 1973), *S. aequalis* (Woodrum and Tarter, 1973; Gatewood and Tarter, 1983), *S. californica* (Azam and Anderson, 1969) and *S. itasca* (Lilly, 1976; Lilly *et al.*, 1978). However, information on life histories for this group of insects has not been reported for southern and subtropical regions. Life history information on alderflies from more southern latitudes would contribute to a better understanding of the ecology of these insects in these regions. The purpose of this study was to estimate the life history and feeding habits of *Sialis* occurring in two different habitats (a reservoir and river) in central Texas.

METHODS AND MATERIALS

Study areas.—Study sites were located at the North Fork of the San Gabriel River (30°38'48.1"N, 97°41'00.7"W) in Georgetown, Williamson County, Texas, and in an impounded section of the Colorado River (30°16'31.9"N, 97°46'17.6"W) known as Town Lake in Austin, Travis County, Texas (Fig. 1).

The San Gabriel River flows eastward through Williamson county primarily through a rural landscape dominated by a limestone substrate. In areas where we collected *Sialis*, depth and width of the river averaged 0.3 m and 15 m, respectively. The river is impounded approximately 4.5 km upstream from the study site so lentic-like conditions sometimes exist because flow may cease or be reduced when the upstream flood gates are closed (Fig. 2). However, the highly variable flows of the river are characteristic of most streams and rivers of central Texas.

The second study location was an impounded section of the Colorado River, which flows eastward through Travis County. The reservoir is long, narrow and maintained at a relatively constant level. The average width, length and depth of the reservoir during this study was approximately 183 m, 9.7 km and 4.3 m, respectively (City of Austin, 1992).

Habitat conditions.—Water temperature (C) and dissolved oxygen concentrations (mg/liter) were measured during the afternoon on each sampling date with a calibrated Orion oxygen meter (Model #840). Measurements were taken above the substrate (about 1 m in Town Lake; 0.3 m in the San Gabriel River) in the habitats where *Sialis* larvae were collected. The Wilcoxon signed-rank test for paired observations ($\alpha = 0.05$; XLSTAT 4.4 statistical software) was used to determine if water temperatures and dissolved oxygen concentrations differed between Town Lake and the San Gabriel River. Because of the relatively small

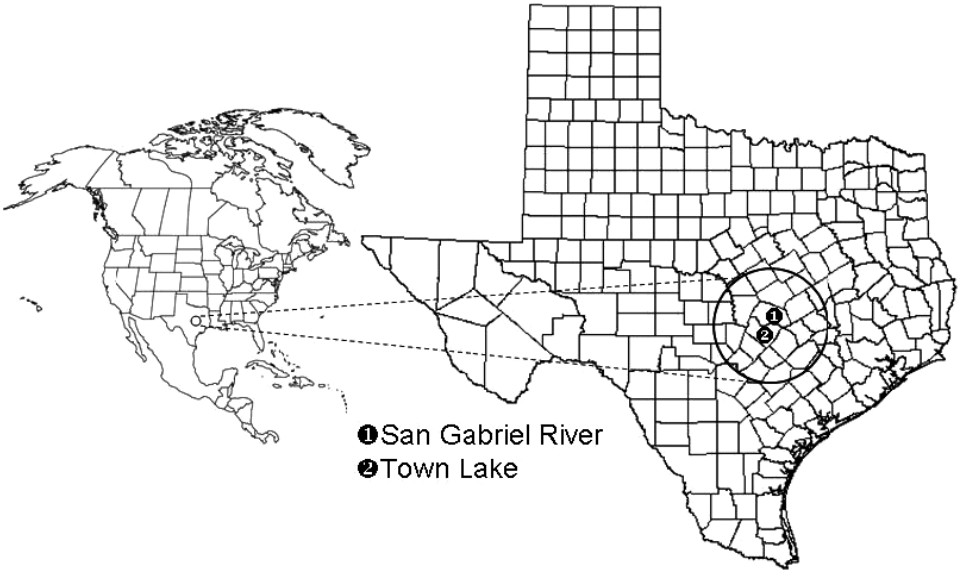


FIG. 1.—Map showing the location of study sites in central Texas

sample sizes ($n = 22$) for the physical-chemical parameters, we opted to use a distribution free statistic for these analyses.

Cumulative water temperatures were determined for each study location to compare the relative seasonal fluctuation patterns in each system. This data was obtained by recording the actual temperatures for each sampling date, and then summing all values for the entire

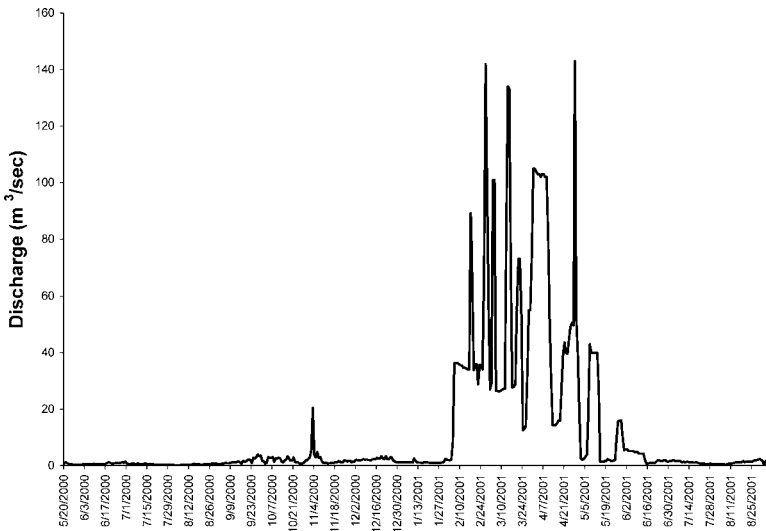


FIG. 2.—Discharge in the San Gabriel River during the study. Data from USGS station 08104700

study period. While this method does not provide annual degree-day values, it does allow for comparison of the relative thermal regimes of the lake and the river.

Sialis collection.—Larval collections were made monthly from May 2000 through September 2001. Larvae were collected by kicking-up debris and sediment within an area approximately 1 m² and sweeping a D-frame collecting net (500 µm mesh) through the disturbed area. The collected materials were preserved in 95% ethanol in the field, and returned to the laboratory and sorted for *Sialis* larvae and associated invertebrates. Head capsule width (mm) of all *Sialis* larvae was measured using a calibrated micrometer mounted in a dissecting microscope. Larval instars were estimated by plotting head capsule widths against numbers collected and then applying Dyar's Rule (Borror *et al.*, 1989) to estimate the larval instar size ranges based on the head capsule widths of first instar larvae (mean = 0.30 mm) and prepupae (mean = 2.33 mm) with a geometric progression factor of 1.2. The head capsule width of first instar larvae was confirmed through hatching field-collected eggs in the laboratory. Life history of *Sialis* in each aquatic ecosystem was estimated by plotting by sample date the proportion of each larval instar present and the occurrence of prepupae and adults.

Prepupae were collected by constructing V-shaped pit-fall traps placed perpendicular to the waters edge (after Azam and Anderson, 1969). Two boards (each 180 cm long, 15.2 cm high and 2.5 cm wide) were placed along the shore 3–8 m from the water. The average opening at the trap mouth was 2.70 m. Mature larvae (prepupae) exiting the water in search of pupation sites were directed into the "V" of the trap where they fell into a collection container (20 cm deep) recessed into the soil. Three traps were placed at the San Gabriel River and two at Town Lake. Traps were checked weekly and sometimes semiweekly from January through April 2001. No preservative was used in the traps. The head capsule widths of trapped prepupae were measured with a calibrated ocular micrometer (mm).

Because flight of sialids generally is limited and infrequent, adults were collected by hand between 3 March and 4 April 2001 while they were resting on terrestrial vegetation or by sweeping with an insect net. Sampling sites were visited weekly from February through May. Collected adults were transported to aquaria in the lab so oviposition could take place. When these adults were found dead in aquaria, they were removed, measured (head capsule width) and preserved in 70% ethyl alcohol.

Twelve egg masses (one on 22 April and 11 on 30 April 2001) were collected at Town Lake, but no egg masses were located at the San Gabriel River. Four gravid females were dissected and five randomly selected eggs per female were measured (mm) under a dissecting microscope for length, width, and micropylar projection. To obtain definitive first instars for head capsule size determinations, one egg mass was removed from an aquarium and placed over water in a separate container to collect newly hatched larvae. Their head capsule widths were measured using the same technique as the field collected larvae.

The gut contents of 84 *Sialis* larvae (61 from the San Gabriel River, 23 from Town Lake; instars IV–X) were analyzed. The dissection process consisted of pinning the larva down with the ventral side up and cutting the abdomen open to remove the crop and intestine. Gut contents were dispersed on a microscope slide and whole prey were identified to the lowest practical taxonomic level and counted under magnification.

RESULTS

Water temperatures for Town Lake and the San Gabriel River varied among sampling dates and location (Fig. 3). For Town Lake, water temperature ranged from 11.9 C (January

2001) to 29.1 C (August 2000), with an annual (first year) mean of 20.1 C. By comparison, water temperatures for the San Gabriel River ranged from 9.6 C (January 2001) to 33.9 C (July 2001), with an annual (first year) mean of 20.1 C. Although there was a general trend of temperatures in the San Gabriel River being warmer during summer months and cooler during winter months in comparison to those of Town Lake (Fig. 3), observed differences in temperature between the two sites were not significantly different (Wilcoxon signed-rank test $T = 1.18$, $P = 0.24$). Cumulative temperatures for the two sampling locations were similar (Fig. 3) with Town Lake having 407.4 C from June 2000 through June 2001 while the San Gabriel River during this same period was 418.9 C.

Dissolved oxygen concentrations in Town Lake ranged from 4.3 mg/liter (August 2001) to 12.1 mg/liter (January 2001), with a mean of 8.5 mg/liter across all sampling dates. In comparison, dissolved oxygen concentrations in the San Gabriel River were significantly higher (Wilcoxon signed-rank test $T = 3.94$, $P = 0.0001$) ranging from 6.1 mg/liter (June 2001) to 15.5 mg/liter (January 2001), with a mean of 11.0 mg/liter across all sampling dates.

Adults of two closely related species of *Sialis* (*S. itasca* Ross and *S. velata* Ross) were collected concurrently from both Town Lake and the San Gabriel River. Although the adult males of these two species can be distinguished, insufficient morphological characters exist by which to separate the adult females and immature stages (Ross, 1937). Therefore, the larval size distribution, life history data and diet analysis from the two collecting sites are presented for the genus only. Although we were unable to differentiate among the immature stages and adult females of the two species of *Sialis* present in our study area, our data indicate they have strongly similar life histories and developmental periods.

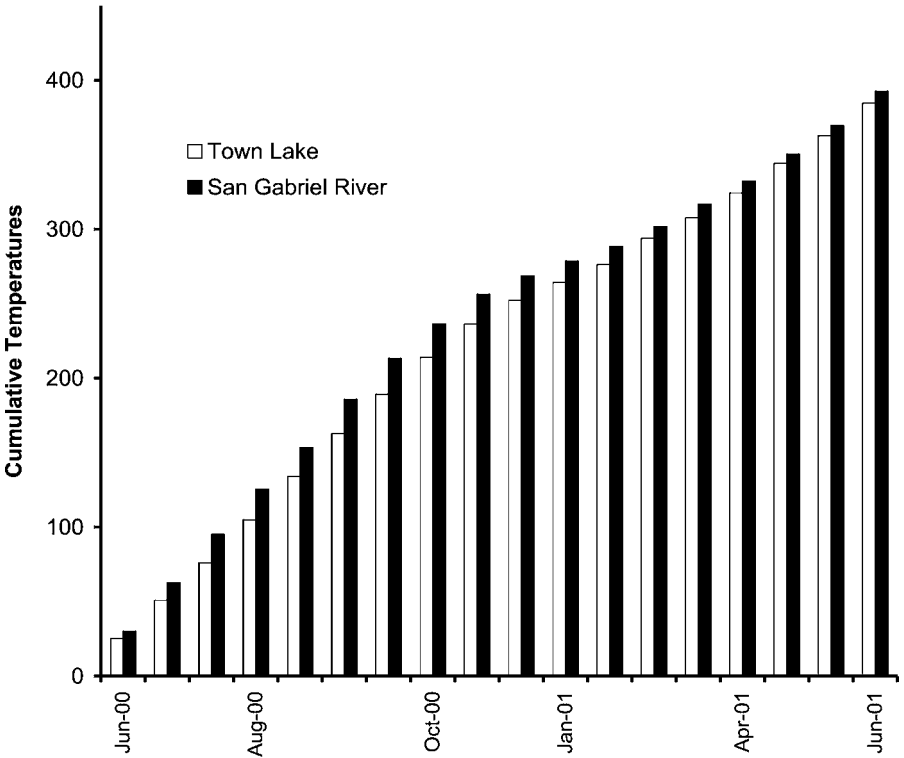
A total of 1197 *Sialis* larvae were collected from Town Lake and the San Gabriel River. The combined size distribution of larval head capsules collected from both sampling locations showed *Sialis* to have ten larval instars with some overlap among size classes (Figs. 4, 5). The seasonal distribution of instars showed *Sialis* at Town Lake and the San Gabriel River to have largely synchronous univoltine life cycles with some overlap among the distribution of larval instars among sampling dates (Fig. 5). Hatching from eggs occurred March–April based on the presence of early instars in April and May 2001 collections. By May, nearly all size classes were present, including final instars. Larvae progressively increased in size from spring through autumn and by November and December, most larvae were in their final instar.

Thirty prepupae were collected in shoreline pit-fall traps from 17 January 2000 through 11 April 2000 (Fig. 6). Twenty specimens collected at Town Lake and 10 from the San Gabriel River had an average head capsule width of 2.33 mm (range from 1.71–2.83). The broader range of head capsule widths observed for prepupae likely reflects sexual dimorphism since female alderflies usually are larger than males (Ross, 1937). The San Gabriel River larvae exhibited prepupal emergence from mid-January through the end of January, whereas Town Lake prepupal emergence occurred from the beginning of March through mid-April (Figs. 5, 6).

Adults were present at the San Gabriel River from 4 March 2001 through 2 April 2001 (Fig. 5). A similar pattern was observed at Town Lake where adults were present from 7 March 2001 until 11 April 2001. Adult head capsule widths ranged from 1.67 mm in both systems to 2.56 mm and 2.63 mm in Town Lake and the San Gabriel River, respectively.

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FIG. 3.—Water temperatures (C) by date and annual accumulations in Town Lake and the San Gabriel River, Texas, June 2000–August 2001



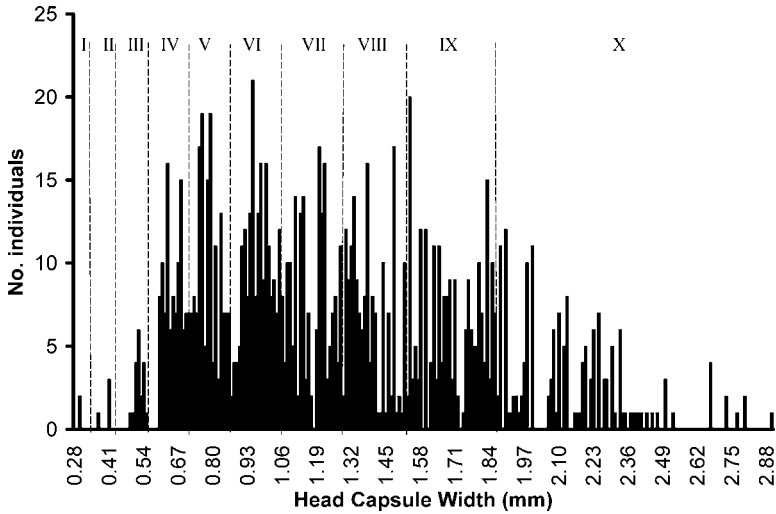


FIG. 4.—Distribution of larval head capsule widths of *Sialis* spp. collected in Town Lake and the San Gabriel River, Texas, June 2000–August 2001. Roman numerals and dashed lined indicate instar size ranges estimated using Dyar's Rule with a geometric progression factor of 1.2

Sexual dimorphism was evident with males (mean = 1.88 mm) being smaller than females (mean = 2.20 mm).

Sialis eggs collected from riparian vegetation at Town Lake ranged from 0.58–0.66 mm in length (mean = 0.66 mm), 0.21–0.35 mm in width (mean = 0.29 mm), with the micropylar projection ranging from 0.09–0.14 mm in length (mean = 0.12 mm). Gravid females ($n = 4$) caught in the field had an average of 352 eggs in their ovaries (range from 61–573). Eleven of the 12 collected egg masses were found on the stems of bald cypress, *Taxodium distichum*, overhanging the water. One egg mass was found attached to a box elder, *Acer negundo*.

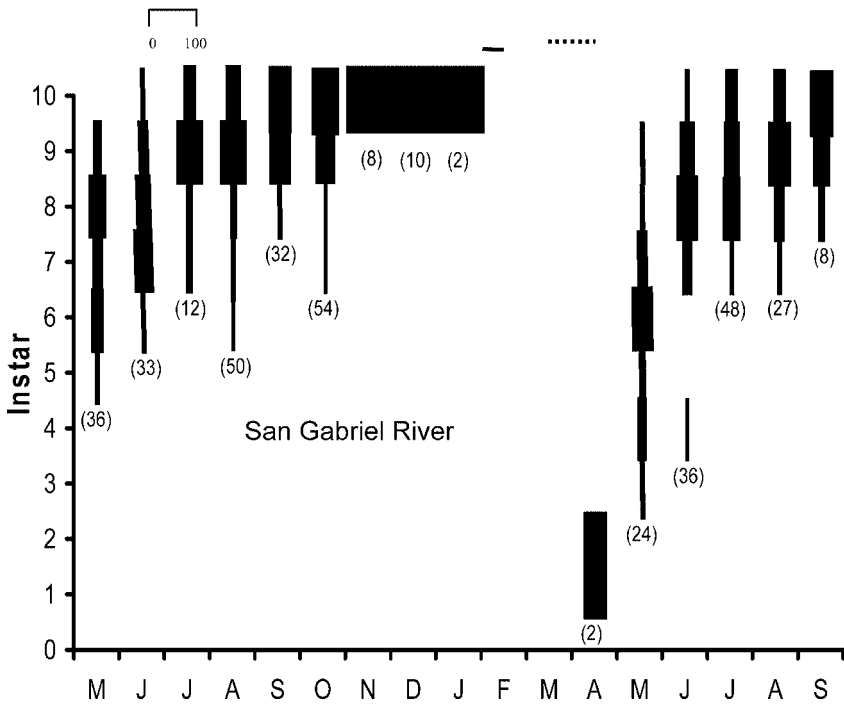
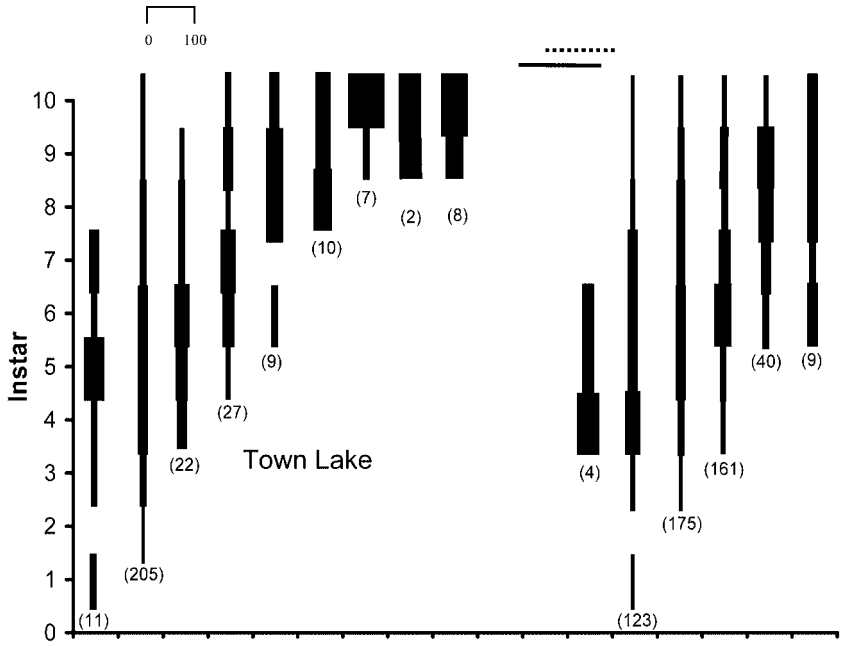
Only three types of prey items were found in the guts of the *Sialis* larvae (instars IV–X) we examined. Of the 84 guts analyzed, 67% were empty and 33% contained food. Larval guts in Town Lake contained 67% ostracods, 22% oligochaetes and 11% chironomids and larvae from the San Gabriel River were similar with 53% ostracods, 38% oligochaetes and 9% chironomids.

DISCUSSION

We found the two coexisting and closely related sister species of *Sialis* from a reservoir and river in central Texas to have 10 larval instars, and the seasonal distribution of immature and adult life stages showed synchronous, seasonal, univoltine life histories with a single cohort. Previous investigations show that univoltine life histories are most common for *Sialis* across most of the United States (Azam and Anderson, 1969; Woodrum and Tarter, 1973; Lilly,

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FIG. 5.—Life history of *Sialis* spp. in Town Lake and the San Gabriel River, Texas, June 2000–August 2001. The width of each bar represents the percentage of each instar collected and numbers under the bars indicate the number of larvae collected that month. Solid lines above the bars indicate the month(s) when prepupae were trapped; dashed lines above the bars indicate when adults were collected



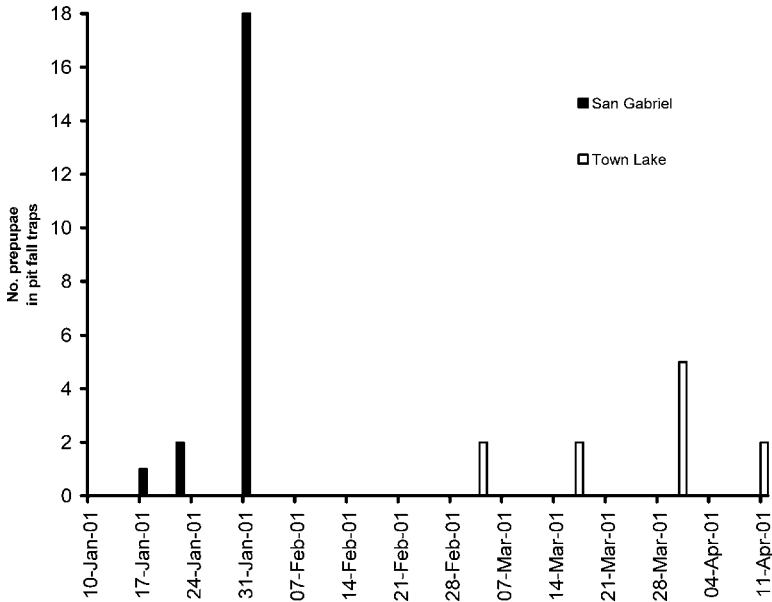


FIG. 6.—Prepupal emergence patterns of *Sialis* spp. at Town Lake and the San Gabriel River, Texas, June 2000–August 2001

1976; Lilly *et al.*, 1978; Gatewood and Tarter, 1983). However, Pritchard and Leischner (1973) found that a population of *S. cornuta* in Canada was semivoltine and studies in France show *S. lutaria* to be univoltine (Iverson and Thorup, 1987) at low latitudes and altitudes, but merovoltine at high altitudes (Giani and Laville, 1973). Short *et al.* (1987) in a study of four central Texas streams found the megalopteran *Corydalus* to be univoltine in three streams, but in a fourth stream with higher summer temperatures, larval development patterns suggested a bivoltine life cycle, not previously reported for this group. The latter studies on life history of Megaloptera are consistent with the many life history studies of aquatic insects that show an inverse relationship between latitude and the number of generations per year (Corbet, 1980; Ward and Stanford, 1982; Brittain, 1983; Ward, 1992; Giller and Malmqvist, 1998). Clearly, water temperature affects voltinism in *Sialis* in the northern parts of their range and at high altitudes by requiring more than one year to complete a life cycle. However, the univoltine life history exhibited by *Sialis* in lentic and lotic habitats in central Texas raises the question of why bivoltine or multivoltine life histories were not observed where water temperatures are much warmer year-round in comparison to more northern areas, where some larvae reached their final instar as early as June and most completed larval development in 5 mo or less. The geographically broad univoltine life history reported thus far for *Sialis*, and the lack of plasticity in the life cycle we observed in this study suggests *Sialis* may have genetic and evolutionary constraints on voltinism flexibility at the southern end of its distribution.

Life histories for many aquatic insects require environmental cues, often in the form of temperature or photoperiod, before further development occurs (Sweeney, 1984). Some mayflies (Ephemeroptera) also are also known to maintain a univoltine life history over a broad latitudinal range with varying temperature regimes (Sweeney *et al.*, 1992). Butler

(1984) suggests that genetic constraints may structure diapause at certain life cycle stages to synchronize critical stages with favorable environmental conditions. Such conditions often include optimal food availability (Georgian and Wallace, 1983; Cummins *et al.*, 1989). The genus *Sialis* is mainly distributed in temperate regions and likely evolved in habitats with distinct seasonal patterns, as opposed to subtropical regions where seasonal patterns are less prominent. Sialids are not abundant in the tropics and only one species has been described in Central America (Henry *et al.*, 1992). Adult emergence of other univoltine aquatic insects in temperate regions largely occurs during the spring and summer when favorable environmental conditions exist for adults and reproduction, and food resources are available for the survival and growth of young instars (Butler, 1984; Hurn and Wallace, 2000). At southern latitudes, such as in Texas, seasonal patterns are not as defined, and, as a consequence, multivoltine and asynchronous life histories are common (Butler, 1984; Jackson and Sweeney, 1995). However, no such life history pattern was shown for *Sialis* in this study. Indeed, semivoltine or merovoltine life histories reported for *Sialis* from colder environments suggests that larvae simply do not grow and mature at a sufficient rate to complete a univoltine life history in those habitats. Final instars are probably affected by environmental cues that stimulate prepupal activity and, unless they reach a critical size, the cues for prepupal emergence do not register. As a result, synchronization of adult emergence occurs in the spring for both the lentic and lotic populations we studied. Synchronization for spring emergence appears to be favorable in temperate regions where seasons are more defined and the chance of emergence occurring during unfavorable conditions is reduced (Ward, 1992). One factor in addition to maximum food availability that may influence the degree of synchrony we observed is that mating and reproductive success may be higher for individuals emerging at about the same time. Adult alderflies are short lived (several days, Ward, 1992) and, therefore, may be under selective pressures greater than those of mayflies for synchronous timed emergence. In contrast to most mayflies, alderflies should be at least an order of magnitude less abundant because of their higher trophic level status as predators. An extended emergence period would further temporally distribute an already low population density and have additional costs related to the likelihood of locating a mate.

Although larval diapause has not been reported in *Sialis*, several studies, including this one, show a decrease or apparent lack of growth towards the later instars during winter (Giani and Laville, 1973; Pritchard and Leischner, 1973; Woodrum and Tarter, 1973; Lilly *et al.*, 1978; Gatewood and Tarter, 1983). Woodrum and Tarter (1973) suggested this lack of larval growth correlated with low water temperatures. Similarly, Giani and Laville (1973) showed *S. lutaria* with three periods of slow to no growth during periods of ice cover during its 3-y life cycle. Although true larval diapause (Chapman, 1998) was not determined in this study, reductions in growth due to reduced water temperatures may have ecological consequences similar to those of a diapause.

In this study, prepupal emergence patterns occurred earlier for the lotic than lentic populations. Although photoperiod is thought to be a major environmental cue for emergence patterns in aquatic insects (Butler, 1984; Nylin *et al.*, 1996), the close proximity of Town Lake and the San Gabriel River sites suggests photoperiod may play a less substantial role than water temperature as an environmental cue for pupation for these populations. However, environmental cues used by insects to trigger developmental phases of their life cycle are complex, often interacting (Tauber *et al.*, 1986) and little studied in aquatic insects (Sweeney, 1984).

The diet of *Sialis* larvae examined in this study was narrow and consisted entirely of chironomids (Diptera, Chironomidae), oligochaetes (Annelida, Oligochaeta) and ostracods

(Crustacea, Ostracoda) although the benthic macroinvertebrate communities in Town Lake and the San Gabriel River were considerably more diverse including amphipods, mayflies, caddisflies and other dipterans (Locklin, 2001). Lilly *et al.* (1978) and Pritchard and Leischner (1973) found similar restricted feeding habits in *S. itasca* and *S. cornuta*, respectively. However, *Sialis* larvae have generally been thought to have diverse opportunistic diets where they feed on the most abundant members of the benthic invertebrate community (Azam and Anderson, 1969; Gianì and Laville, 1973; Hildrew and Townsend, 1976). Prey items in those studies include members of the Ephemeroptera, Trichoptera, Diptera and aquatic Acari. Also, organic detritus and filamentous algae have been reported in the guts of *Sialis* (Woodrum and Tarter, 1973; Gatewood and Tarter, 1983).

Many (67%) of the larval guts examined in this study were empty and this finding is not uncommon. Pritchard and Leischner (1973) found the rate of digestion is dependent on water temperature, and the amount of time after ingestion until the first fecal pellet is produced was 106 h at 5 C, 29 h and 12.5 C, and 22 h at 17.5 C. The water temperatures of the San Gabriel River and Town Lake reported here suggest that digestion probably is quite rapid in these systems. *Sialis* larvae can live up to 2 mo without food (Azam and Anderson, 1969) and this may help explain the high percentage of empty guts in these studies. For these reasons, we chose not to calculate prey selection coefficients because some soft bodied prey may not have been detected in our analysis, and the data likely would not have yielded statistically robust results.

Our results suggest voltinism for the genus *Sialis* varies little with southern geographic location and warmer water temperatures and is largely univoltine. This study also showed that life history for these primitive holometabolous insects did not differ substantially among broadly different habitats and ecological conditions. Such a narrow range of responses over such a broad range of conditions indicates that evolutionary/genetic constraints may play a more significant role in regulating aspects of life history of *Sialis* than environmental factors. Similar patterns may be characteristic of megalopterans in general compared to more recent holometabolous groups where voltinism in many taxa (Jackson and Sweeney, 1995) tends to increase in areas where water temperatures are warmer year round.

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LITERATURE CITED

- AZAM, K. M. AND N. H. ANDERSON. 1969. Life history and habits of *Sialis rotunda* and *S. californica* in western Oregon. *Ann. Entomol. Soc. Am.*, **62**:549–558.
- BORROR, D. J., C. A. TRIPLEHORN AND N. F. JOHNSON. 1989. An Introduction to the study of insects, 6th ed. Saunders College Publishing, Fort Worth, Texas. 875 p.
- BOWLES, D. E. 1990. Life history and variability of secondary production estimates for *Corydalis cornutus* (Megaloptera: Corydalidae) in an Ozark stream. *J. Agric. Entomol.*, **7**:61–70.
- BRITAIN, J. E. 1983. The influence of temperature on nymphal growth rates in mountain stoneflies (Plecoptera). *Ecology*, **64**:440–446.
- . 1990. Life history strategies in Ephemeroptera and Plecoptera, p. 1–12. *In*: I. C. Campbell (ed.). Mayflies and Stoneflies. Kluwer Academic Publishers, New York. 366 p.
- BROOKER, M. P. 1979. The life cycle and growth of *Sialis lutaria* L. (Megaloptera) in a drainage channel under different methods of plant management. *Ecol. Entomol.*, **4**:111–117.
- BUTLER, M. G. 1984. Life histories of aquatic insects, p. 24–55. *In*: V. H. Resh and D. M. Rosenberg (eds.). The ecology of aquatic insects. Praeger Publishing, New York. 625 p.

- CHAPMAN, R. F. 1998. The insects: structure and function, 4th ed. Cambridge University Press, Cambridge, United Kingdom. 770 p.
- CITY OF AUSTIN. 1992. Diagnostic study of water quality conditions in Town Lake, Austin, Texas. City of Austin, Environmental and Conservation Services Department, Environmental Resource Management Division COA-ERM/WRE 1992-01.
- CORBET, P. S. 1980. Biology of Odonata. *Annu. Rev. Entomol.*, **25**:189–217.
- CUMMINS, K. W., M. A. WILZBACH, D. M. GATES, J. B. PERRY AND W. B. TALLIAFERRO. 1989. Shredders and riparian vegetation. *Bioscience*, **39**:24–30.
- ELLIOT, J. M. 1996. Temperature-related fluctuations in the timing of emergence and pupation of Windermere alder-flies over 30 years. *Ecol. Entomol.*, **21**:241–247.
- FLINT, O. S., JR. 1964. New species and new state records of *Sialis* (Neuroptera: Sialidae). *Entomol. News*, **75**:9–13.
- GATEWOOD, R. W. AND D. C. TARTER. 1983. Life history and ecology of the alderfly *Sialis aequalis* Banks, from Flatfoot Creek, Mason County, West Virginia. *Proc. West Virginia Acad. Sci.*, **55**:102–113.
- GANI, N. AND H. LAVILLE. 1973. Cycle biologique et production de *Sialis lutaria* L. (Megaloptera) dans le lac de Port-Bielh (Pyrenees Centrales). *Ann. Limnol.*, **9**:45–61.
- GILLER, P. S. AND B. MALMQVIST. 1998. The biology of streams and rivers. Oxford Univ. Press, New York. 296 p.
- GEORGIAN, T. AND J. B. WALLACE. 1983. Seasonal production dynamics in a guild of periphyton-grazing insects in a southern Appalachian stream. *Ecology*, **64**:1236–1248.
- HAYASHI, F. 1988. Life history variation in a dobsonfly, *Protohermes grandis* (Megaloptera: Corydalidae): effects of prey availability and temperature. *Freshwat. Biol.*, **19**:205–216.
- . 1996. Life cycle of *Protohermes immaculatus* (Megaloptera: Corydalidae) accelerated by warm water overflowing a dam. *Aquat. Insects*, **18**:101–110.
- . 1997. A new species of *Sialis* (Megaloptera: Sialidae) from Japan. *Jap. J. Entomol.*, **65**:813–815.
- HENRY, C. H., N. D. PERRY AND P. A. ADAMS. 1992. The neuropteroid orders of Central America, p. 432–458. *In*: D. Quintero and A. Aiello (eds.). Insects of Panama and Mesoamerica. Oxford University Press, Oxford. 692 p.
- HILDREW, A. G. AND C. R. TOWNSEND. 1976. The distribution of two predators and their prey in an iron-rich stream. *J. Animal. Ecol.*, **45**:41–57.
- HURYN, A. D. AND J. B. WALLACE. 2000. Life history and production of stream insects. *Annu. Rev. Entomol.*, **45**:83–110.
- IVERSON, T. M. AND J. THORUP. 1987. Population dynamics and production of *Sialis lutaria* L. (Megaloptera) in the Danish River Susa. *Freshwat. Biol.*, **17**:461–469.
- JACKSON, J. K. AND B. W. SWEENEY. 1995. Egg and larval development times for 35 species of tropical stream insects from Costa Rica. *J. N. Am. Benthol. Soc.*, **14**:115–130.
- KNIGHT, A. W. AND M. A. SIMMONS. 1975. Factors influencing the oxygen consumption of the hellgrammite, *Corydalus cornutus* (L.) (Megaloptera: Corydalidae). *Comp. Biochem. Physiol.*, **50A**:827–833.
- LILLY, C. K. 1976. Ecological life history and the pH tolerance of a pond sialid, *Sialis itasca* Ross, from West Virginia (Insecta: Megaloptera). Unpublished M.S. Thesis, Marshall University, Huntington, West Virginia.
- , D. L. ASHLEY AND D. C. TARTER. 1978. Observations on a population of *Sialis itasca* Ross in West Virginia (Megaloptera: Sialidae). *Pysche*, **85**:209–217.
- LOCKLIN, J. L. 2001. Life history of the alderfly, *Sialis* (Megaloptera: Sialidae), in Town Lake and the San Gabriel River in central Texas with a key to the species occurring in Texas. Unpublished M.S. Thesis, Texas State University–San Marcos, San Marcos, Texas.
- NYLIN, S., K. GOTTHARD AND C. WIKLUND. 1996. Reaction norms for age and size at maturity in *Lasiommata* butterflies: predictions and tests. *Evolution*, **50**:1351–1358.
- PRITCHARD, G. AND T. G. LEISCHNER. 1973. The life history and feeding habits of *Sialis cornuta* Ross in a series of abandoned beaver ponds (Insecta; Megaloptera). *Can. J. Zool.*, **51**:121–131.
- ROSS, H. H. 1937. Nearctic alder flies of the genus *Sialis* (Megaloptera: Sialidae). *Bull. Illinois Nat. Hist. Surv.*, **21**:57–99.

- SHORT, R. A., E. H. STANLEY, J. W. HARRISON AND C. R. EPPERSON. 1987. Production of *Corydatus cornutus* (Megaloptera) in four streams differing in size, flow, and temperature. *J. N. Am. Benthol. Soc.*, **6**:105–114.
- SMOCK, L. A. 1988. Life histories, abundance and distribution of some macroinvertebrates from South Carolina, USA coastal plain stream. *Hydrobiologia*, **157**:193–208.
- SWEENEY, B. W. 1984. Life histories of aquatic insects, p. 56–100. *In*: V. H. Resh and D. M. Rosenberg (eds.). *The ecology of aquatic insects*. Praeger Publishing, New York. 625 p.
- , J. K. JACKSON, J. D. NEWBOLD AND D. H. FUNK. 1992. Climate change and the life histories and biogeography of aquatic insects in eastern North America, p. 143–176. *In*: P. Firth and S. G. Fisher (eds.). *Global climate change and freshwater ecosystems*. Springer-Verlag Inc., New York. 321 p.
- TAUBER, M. J., C. A. TAUBER AND S. MASAKI. 1986. *Seasonal adaptations of insects*. Oxford University Press, New York, New York. 411 p.
- TOWNSEND, L. H. 1939. A new species of *Sialis* (Megaloptera, Sialidae) from Kentucky. *Proc. Entomol. Soc. Wash.*, **41**:224–226.
- WARD, J. V. AND J. A. STANFORD. 1982. Thermal responses in the evolutionary ecology of aquatic insects. *Annu. Rev. Entomol.*, **27**:97–117.
- . 1992. *Aquatic insect ecology: biology and habitat*. John Wiley and Sons, Inc., New York. 452 p.
- WHITING, M. F. 1991a. New species of *Sialis* from Southern California (Megaloptera: Sialidae). *Great Basin Nat.*, **51**:411–413.
- . 1991b. A distributional study of *Sialis* (Megaloptera: Sialidae) in North America. *Entomol. News*, **102**:50–56.
- WOODRUM, J. E. AND D. C. TARTER. 1973. The life history of the alderfly, *Sialis aequalis* Banks, in an acid mine stream. *Am. Midl. Nat.*, **89**:360–368.

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