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

THESIS

Presented to the Graduate Council of
Southwest Texas State University
in Partial Fulfillment of
the Requirements

For the Degree

Master of Science

by

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San Marcos, Texas

December 2001

Acknowledgments

I wish to extend my sincere gratitude to Dr. Tom Arsuffi, my thesis advisor, and Dr. David Bowles for their guidance, encouragement, and assistance during my graduate work and the preparation of this manuscript. I'd also like to thank Dr. Glenn Longley and Evan Hornig for serving on my thesis committee and critically reviewing this manuscript. I also thank my first biology professor, Dr. Ben Liles, for that first influential biology course and for his continued interest in my academic and personal development.

Many thanks to Joe Martin, Anna Moehrig, Chad Norris, Steven Tschoerner, Bruce Kelley, and Connie Johnson for their assistance in the field and/or lab. An extended thanks to Dr. John Abbott and the Brackenridge Field Laboratory (BFL), University of Texas, for granting me access to Town Lake and Dr. Don Tarter, Marshall University, for loaning me specimens of *Sialis* from West Virginia.

I personally wish to thank my parents for their continuous support, patience, and sacrifices for my educational endeavors. I can never repay their incessant support. And finally, to my fiancée Anna who always encourages and supports everything I do, this thesis is dedicated to you.

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INTRODUCTION

The order Megaloptera is among the most primitive group of winged insects in the world (Chandler 1971, Whiting 1994). They undergo complete metamorphosis with aquatic larvae, and terrestrial eggs, pupae, and adults. Megalopterans spend most of their life cycle in water and therefore are considered an aquatic order. There are two families of Megaloptera: the Sialidae and the Corydalidae. The Sialidae are widely distributed in the world (Hayashi 1997) and are commonly called alderflies because adults can often be found resting on alders and other vegetation adjacent to streams. As adults, sialids are fairly uniform in size and overall appearance (Whiting 1994). They are dark colored (Chandler 1971) with a forewing of 15mm or less and a body length of about 25mm or less (Evans and Neunzig 1996). Females lay their eggs in masses on leaves or other structures overhanging the larval aquatic habitat (Ross 1937, Chandler 1971, Evans and Neunzig 1996). Habitat selection results from the female's choice of oviposition sites (Azam and Anderson 1969), which are usually within one to two meters above the water. Most eggs hatch between 7 and 21 days, with the larvae in their fifth to sixth (out of ten) instar by winter (Pritchard and Leischner 1973). Eggs hatch at night (Chandler 1971) and most of the eggs in the mass hatch in the same night (Evans 1972, Pritchard and Leischner 1973). Larvae are campodeiform (Borror et al. 1989) and have seven pairs of lateral abdominal filaments and a long terminal filament (Ross 1937, Flint 1973, Evans and Neunzig 1996). They are generally abundant in streams, lakes, and reservoirs if the substrate is soft and detritus is abundant (Evans 1972, Iversen and Thorup 1987, Elliot 1996, Evans and Neunzig 1996). In lakes, they tend to aggregate in the littoral region where debris and detritus accumulate (Canterbury 1978). When hatchlings fall into the water, they are immediately active swimmers (Pritchard and Leischner 1973, Elzinga 1997). Chandler (1971) and Canterbury and Neff (1980) found larvae pass through as many as 10 instars during a one or two year life cycle, whereas Giani and Laville (1973) found larvae with a three-year life cycle. They generally are opportunistic burrowing predators that feed in the dark (Chandler 1971) on a wide variety of aquatic invertebrates (Azam and Anderson 1969, Giani and Laville 1973, Hildrew and Townsend 1976, Phillips 1996). The burrows are usually J or U shaped (Chandler 1971, Wang et al. 2001) and once the prey is captured, they ingest it whole (Pritchard and Leischner 1973). Larvae inhabit the burrows for lengthy periods of time and consequently must re-oxygenate them. To accomplish this, larvae undulate the abdomen to create a current of water from the openings in the burrows. Irrigation of oxygenated water into the burrows increases with increasing temperatures (Wang et al. 2001). As a result of their ability to irrigate their burrows, *Sialis* larvae can tolerate moderate eutrophication (Wiederholm 1984). Larvae have been found to live up to two months without food, indicating a survival capability when prey density is low and then to rapidly develop when food is abundant (Azam and Anderson 1969). Prey items reported include tubificid worms, chironomid larvae and pupae, ostracods, Ephemeroptera, Trichoptera, Ceratopogonidae, Empididae, Tipulidae, Dytiscide, Copepods, and aquatic mites (Pritchard and Leischner 1973). Sialid larvae are prey for odonates (Lilly et al.

1978), dobsonflies (Corydalidae), bluegill sunfish, *Lepomis macrochirus* (Evans 1972), perch, *Perca fluviatilis* (Diehl 1995), and trout, *Salmo trutta* (Giani and Laville 1973). When larvae are mature, they migrate to the bank above the water level and burrow into the ground (1-10cm) where they form an earthern cell to pupate (Chandler 1971, Evans 1972, Evans and Neunzig 1996). Adults in temperate regions emerge from late spring to early summer (Evans and Neunzig 1996) and probably do not feed (Ross 1937, Elzinga 1997). Since flight is limited and infrequent, they usually remain in the same area where emergence occurred (Evans and Neunzig 1996). Mating takes place on leaves, stems, and twigs of shoreline vegetation (Canterbury 1978) during the day (Ross 1937). To mate, the male positions himself under the female's abdomen from the rear and raises his abdomen so their respective genitalia come into contact. A spermatophore is then passed to the female and copulation is complete. Oviposition occurs within a day (Evans 1972).

The family Sialidae has nine genera worldwide, including *Austrosialis* (2 spp.), *Haplosialis* (1), *Indosialis* (2), *Leptosialis* (1), *Nipponsialis* (1), *Proindosialis*, (1), *Protosialis* (8), *Sialis* (51), and *Stenosialis* (2) (Whiting 1994). The only genus found in the United States and Canada is *Sialis*, which is also distributed throughout Europe, Egypt, Japan, and China (Whiting 1994, Hayashi 1997). There are 23 known species in North America (Ross 1937, Whiting 1991). Ross (1937) divided the Nearctic species into four groups based on genital characteristics. These include the *californica* group, the *infumata* group, the *aequalis* group, and the *americana* group (Ross 1937). In Texas, species from two of the groups have been reported (Whiting 1991). *Sialis velata* and *S. itasca* belong in the *infumata* group, which is characterized by the male genitalia having long, hooked mediunci. *Sialis americana* belongs in the *americana* group, characterized by the male genitalia having long, straight mediunci. Although only three species of Sialis have been reported from Texas, the distribution of additional species in neighboring states suggests the likelihood that they may eventually be found in Texas. These species include *S. vagans* (AR, OK), *S. mohri* (AR), *S. joppa* (AR, LA, OK), and *S. infumata* (AR, OK) (Whiting 1991). Although *Sialis* occurs in the southern regions of the United States, relatively little is known about them in Texas. The majority of the studies have been conducted in the northeastern and northwestern regions of North America. With the possibility of at least seven species inhabiting Texas aquatic ecosystems, more information on their ecology, life history characteristics, and distributional relationships are needed.

Life history may be defined as the events that govern the reproduction and survival of a species or a population (Butler 1984). Life history characteristics influence the progression from one stage to another in the life cycle. Life cycle and life history are often used interchangeably, but life cycle is considered qualitative because it simply describes the sequence of respective morphological stages (e.g., egg - pupa - larva - adult) (Butler 1984). Life history, however, includes both qualitative and quantitative information and includes fecundity, development, longevity, rate of growth, feeding, habitat, behavior, etc. (Butler 1984, Epperson and Short 1987). While life cycles are fixed for a given group, life history can often vary (Butler 1984, Giller and Malmqvist 1998).

Life history information is important in understanding the functional roles of macroinvertebrates in aquatic environments. 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, including those related to climate change caused by anthropogenic atmospheric changes or the result of other human activities like river regulation, reservoir construction, thermal discharge, deforestation, and changes in land use (Elliot 1996). Two aspects of the life history are of particular interest: voltinism and phenology (Giller and Malmqvist 1998). Voltinism refers to the number of generations produced in a year for a given species. Six types of voltinism (univoltine, bivoltine, trivoltine, semivoltine, multivoltine, and merovoltine) are recognized (Butler 1984). While it was originally thought that most aquatic insects were univoltine (Hynes 1970), it is now known that voltinism varies widely among these animals (Butler 1984). Phenology refers to the seasonal timing to complete the various life cycle stages (Giller and Malmqvist, 1998), such as egg hatching, prepupal and adult emergence, pupation length, and larval growth rates.

Life history patterns among closely related species are generally similar, but phenology and voltinism often vary in different ecosystems with different environmental conditions (Butler 1984, Smock, 1988). Environmental factors, such as temperature, food, and photoperiod are thought to be responsible for most life history variations found in closely-related species (Butler 1984, Sweeney 1984, Sweeney et al. 1992, Giller and Malmqvist, 1998). Temperature affects many life history aspects of aquatic insects (Ward and Stanford 1982, Butler 1984, Sweeney et al. 1992) and tends to be inversely related to the duration of egg, pupal, and larval development (Short et al. 1987, Hayahsi 1988, 1996; Wagner 1990, Elliot 1996, Giller and Malmqvist 1998). As a result, geographical location becomes an important consideration when evaluating life histories for organisms having wide distributional patterns. For example, for species at northern latitudes in 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 six months in central Texas while Knight and Simmons (1975) reported development taking three to four years in Michigan. 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. Trichoptera in central Texas are multivoltine as opposed to univoltine or sometimes bivoltine in more temperate areas (Tiemann and Arsuffi

1991). In addition to latitudinal variation in voltinism, altitude also has effects. Iversen and Thorup (1987) reported a univoltine life history for *Sialis lutaria* in Denmark while Giani and Laville (1973) found them to be merovoltine at higher altitudes in mountainous areas of France. However, variation in life history is not only limited to differences in latitude or altitude, but can also occur locally in streams or rivers with different temperature regimes. Hayashi (1996) found accelerated larval development for *Protohermes grandis* in a stream fed by warmer waters overflowing a top-releasing dam. Short et al. (1987) found different phenologies for *Corydalus cornutus* in central Texas where first instars occurred in the early spring in a warm river and early summer to fall in a cooler spring-fed system.

Life history studies have been completed for several species of *Sialis*. These include *S. rotunda* (Azam and Anderson 1969), *S. lutaria* (Brooker 1979, 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, all of these studies were conducted at northern latitudes. No life history studies of *Sialis* have been reported from the southern region of the United States, including central Texas where the climate varies from Mediterranean to subtropical. Previously, the southern-most studies on the group were in West Virginia (Woodrum and Tarter 1973, Lilly 1976, Tarter et al. 1978, Gatewood and Tarter 1983).

Two species of *Sialis* occur in the current study area: *Sialis itasca* Ross and *Sialis velata* Ross. Both species are widely distributed across the United States and Canada, but Texas represents their southern-most known range. These two species of *Sialis* coexist together in both Town Lake and the San Gabriel River. The purpose of this study is to determine the life history, food habits, and distribution of *Sialis* in a lentic (reservoir) and lotic ecosystem in central Texas. A taxonomic key to the species occurring or possible occurring in Texas and assessment of their geographic distributions also are presented.

DISTRIBUTION

Sialis velata

Sialis velata is distributed from 116° longitude to the East Coast and from the 47th parallel (Roy and Hare 1998) to 30° latitude. Ross (1937) originally reported *S. velata* occurring in 15 U.S. states (Illinois, Kansas, Maine, Maryland, Massachusetts, Michigan, Missouri, New Hampshire, New York, North Dakota, Texas, Virginia, West Virginia, District of Columbia, and Wisconsin) and 4 Canadian provinces (Manitoba, Ontario, Quebec, and Saskatchewan). Additional records of the species have been reported from Nebraska, North Carolina, Tennessee, Vermont (Tarter et al. 1978), Colorado, Idaho, Kentucky, Minnesota, Montana, New Jersey, Oklahoma, Utah, and Wyoming (Whiting 1991). In Texas, records from Kerr (Ross 1937), Bexar, and Travis counties (Whiting 1991) have previously been reported. This is the first report of *S. velata* occurring in Williamson County.

Sialis itasca

Sialis itasca ranges from 98° longitude to the east coast and from 45°latitude to 30° latitude. Tarter et al. (1978) added distributional records of this species to Ross' (1937) monograph including Arkansas, Georgia, Illinois, Indiana, Kansas, Maryland, Michigan, Minnesota, Missouri, New York, North Carolina, North Dakota, Oklahoma, Ohio, Pennsylvania, Tennessee, Texas, Virginia, West Virginia, Wisconsin, and the District of Columbia. The Texas record was from

Brazos County. This is the first report of the species occurring in Williamson and Travis counties, Texas.

DESCRIPTION OF THE STUDY AREAS

Populations of *Sialis* were studied in the North Fork of the San Gabriel River (30° 38' 48.1" N, 97° 41' 00.7" W), Georgetown, Texas and in an impounded section of the Colorado River (30° 16' 31.9" N, 97° 46' 17.6" W), Town Lake, Austin, Texas.

The San Gabriel River originates in Burnet County and consists of four forks: North, Russell, Middle, and South. The river flows eastward roughly 193 km through Williamson and Milam counties through wooded areas over limestone to its confluence with the Little River. There are two major dams on the San Gabriel River: One creates Lake Georgetown (241 meters above sea level) and the second creates Granger Lake (156 meters above sea level). The river, due to Lake Georgetown's dam, is sometimes lentic-like in flow in the sense that flow may sometimes cease or be reduced in dry conditions when the flood gates upstream are closed. As a result, flows can be substantially reduced during the summer months in habitats where *Sialis* occur. However, the highly variable flows of the river are somewhat characteristic of most streams and rivers of central Texas. Discharge (Fig. 6) shows the variable nature and intensity of the river during the study. The section of river sampled is located in the North Fork just west of Interstate Highway 35 in Georgetown.

The second study location was an impounded section of the Colorado River, which flows eastward through Travis County. In 1960, the Longhorn Dam was built to create Town Lake (130 meters above sea level) for flood control and recreation. It is the last of seven lakes in the Highland Lake series extending through the Texas Hill Country. Town Lake extends from the Tom Miller Dam, which forms Lake Austin on the west side of Austin, to the Longhorn Dam in east Austin. The reservoir is a long, narrow, constant level reservoir. The average width of the reservoir is approximately 183 meters and the length is about 9.7 km. The mean depth of Town Lake is 4.27 meters (ranging from 3 meters in the upstream areas and over 9 meters near the dam) (City of Austin 1992). *Sialis* were collected generally from the wadeable areas on the north shoreline along a 1.5 km stretch from the Brackenridge Field Laboratory (University of Texas) to the Loop 1 (Mopac) Highway.

MATERIALS AND METHODS

Habitat Conditions

Water temperature (°C) and dissolved oxygen concentrations (mg/L) were measured on each sampling date (afternoon) with a calibrated Orion oxygen meter (Model #840). Measurements were taken just above the substrate (about 1 m in depth for Town Lake; 0.30 m in depth at the San Gabriel River) in the habitats where *Sialis* larvae were collected (Fig. 8). Degree days were calculated using the following procedure: The temperature recorded at each sampling date was used as the daily average since only one temperature reading was collected. To estimate temperatures for the days not sampled, temperature data collected between successive sampling dates were averaged and applied to the interceding dates. While this method does not provide exact annual degree-day values, it allows a thermal comparison of Town Lake with the San Gabriel River. Friedman's non-parametric ANOVA (α=0.05) (SPSS) was used to determine if water temperatures differed between Town Lake and the San Gabriel River. Water flow at the San Gabriel River was determined using a Flo-mate (Model #2000) flow meter on 27 June 2000, 11 November 2000, and 5 March 2001. Flow at Town Lake was not measurable. Discharge data for the San Gabriel River was obtained from the United States Geological Survey (USGS). Water samples were collected and analyzed for NO_3, O-PO_4, T-PO_4, conductivity, TSS, and turbidity on 2 April 2001.

Larvae

Collections were made semimonthly from May 2000 through October 2000 and April 2001 through September 2001, and monthly from November 2000 through March 2001. A total of 1,197 larvae were collected and measured (head capsule width) to determine instar numbers and sizes over monthly intervals which were used to estimate growth. Larvae were collected using an aquatic hand-held D-frame net. The procedure consisted of kicking up debris and sediment and sweeping the net through the disturbed area. The collected materials were preserved in 95% ethanol. In the laboratory, larvae were separated from the debris by placing all the material in a water-filled white sorting tray. The sorted larvae were stored in 70% ethanol. The debris was then placed back in storage for later sorting of possible prey items. *Sialis* larvae head capsule widths were measured (mm) using a calibrated micrometer mounted in a dissecting microscope for instar determination and growth analysis. First instar larvae were hatched in the laboratory from field-collected eggs to provide a reference point for determining instar ranges. Dyar's Rule, the geometric progression of head capsule growth of 1.2X (Borror et al. 1989) was used to estimate the larval instar size ranges starting with first instar head capsule width (0.30mm) and prepupal head capsule width (2.33mm).

Feeding Habits

The gut contents of 84 *Sialis* larvae (instars IV - X) were analyzed. The dissection process consisted of pinning the larva down with the ventral side up. The abdomen was split open to remove the crop and intestine. Prey contents of the crop and intestine were identified and counted using dissecting and compound microscopes.

To determine possible prey for *Sialis*, the debris collected in the net while sampling for larvae was preserved in 95% ethanol. Each sample was subsampled by randomly removing about 100 prey individuals to determine possible prey composition at each sampling date. Size of the prey was not measured in this study and all organisms were considered possible prey.

Habitat Preference experiment

Some larvae were collected in filamentous algal mats suspended in the water column at Town Lake. To determine whether the larvae preferred sediments or algae, replicated (3) 37.9-litter aquaria were set-up with water and sediment collected from Town Lake. Each aquarium received about 1.5 cm of sediment. Half of the aquarium was supplied with the filamentous algae suspended over the sediment and reaching the water surface while the other half had only exposed sediments. Aquarium heaters maintained water temperatures at 28 C° (about the temperature of Town Lake at the time of the experiment). Aquaria were placed near windows in the lab to expose them to the ambient photoperiod. Six larvae were introduced into the middle of each aquarium and were collected six days later.

Pupae

Mature larvae leaving the water to pupate (prepupae) were collected by constructing V-shaped pit-fall traps placed perpendicular to the waters edge (Fig. 9) (Azam and Anderson 1969). Two boards were placed along the shore where they directed larvae into the "V" of the trap where they fell into a collection container recessed into the soil. The boards were 180 cm long, 15.2 cm high, and 2.5 cm wide. Traps were placed between 3-8 m from the water's edge. The average opening at the trap mouth was 2.70 m. 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. Seven of the trapped prepupae were placed in an aquarium with sand that was sprayed daily to maintain adequate moisture for observations. No adults emerged in the aquaria, however. The head capsule widths of remaining trapped prepupae were measured with an ocular micrometer (mm).

Adults

Adults were collected by hand 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. A paired T-test was used to analyze size differences in males and females. One egg mass was removed from an aquarium and placed over water in a separate container so first instars could be collected.

Eggs

Twelve egg masses were collected in the field at Town Lake. In spite of intensive searching at the San Gabriel River, no egg masses were located. Four gravid females were also dissected and five eggs per female were randomly selected and removed. The egg lengths, widths, and micropylar projections were measured (mm) under a dissecting microscope.

Taxonomic Key

A key to the adult male sialids reported from or possibly occurring in Texas was prepared following Ross (1937). There are several counties in Texas which have larval sialid records (Fig. 15; Appendix I). Since larvae cannot be accurately identified to species, it is likely that some species reported in Louisana, Oklahoma, and Arkansas may occur in those Texas counties. Therefore, a key to the adult male *Sialis* occurring in this region will be useful for discerning the taxonomic composition of additional specimens collected in future studies. All drawings were modified from Ross (1937) and terminology follows Whiting (1994). Additional North American distributional records of the six species occurring in or near Texas are presented in Appendix II.

RESULTS & DISCUSSION

Habitat Conditions

Town Lake

Water temperatures (Fig. 1) ranged from 11.9 C° (January 2001) to 29.1 C° (August 2000), with an annual (first year) mean of 20.1 C°. The estimated annual degree days (above 0 C°) from June 2000 through June 2001 was 7,277 (Fig. 2). Dissolved oxygen concentrations ranged from 4.3 mg/L (August 2001) to 12.1 mg/L (January 2001), with an annual mean of 8.5 mg/L. Additional physical parameters are summarized in Appendix 3.

San Gabriel River

Water temperatures (Fig. 1) ranged from 9.6 (January 2001) to 33.9 C° (July 2001), with an annual (first year) mean of 20.1 C°. The estimated annual degree days the first year was 7,242 (Fig. 2). Dissolved oxygen concentrations ranged from 6.1 mg/L (June 2001) to 15.5 mg/L (January 2001), with an annual mean of 11.0 mg/L. Flow was measured at 4 cm/s on 27 June 2000, 2 cm/s on 17 November 2000, and 30 cm/s on 5 March 2001. Discharge during the study ranged from 0.15 m^3/s to 142 m^3/s (Fig. 6). Additional physical parameters are summarized in Appendix 3.

Comparisons

Both Town Lake and the San Gabriel River had annual mean temperatures of 20.1°C and similar annual degree days. Ward and Stanford (1982) and Ward (1992) noted that while annual degree days can be similar, quite different ranges and seasonality in temperatures may occur. Such differences were found between Town Lake and the San Gabriel River (Friedman's test, $\chi^2 = 74.9$, $p<0.0001$). Town Lake was warmer in the winter and cooler in the summer compared to the San Gabriel River and had markedly less variability. The San Gabriel River had a peak temperature of 33.9° C in July and a low temperature of 9.6° C in January, resulting in a range of 24.3° C. In contrast, Town Lake's maximum temperature of 29.1° C in August and minimum temperature of 12° C in December resulted only in a range of 17.1°C. Flow rates in the San Gabriel River ranged from constant low flows to variably moderate flows, depending on the season (Fig. 6). Town Lake does not experience high intense flow patterns nor appreciable variation in water level since the Lower Colorado River Authority regulates discharge through dams located upstream and downstream.

Larvae

Larvae were found from April through January in both Town Lake and the San Gabriel River. This 10-month larval period in central Texas was similar to larval phenologies for *S. aequalis* in West Virginia of 10.5 months (Gatewood and Tarter 1983) and *S. lutaria* in Denmark of 11 months (Iverson and Thorup

1987). First instars of *S. itasca* in West Virginia were not found until mid-May (Lilly et al. 1978), whereas in this study first instars (0.30 mm) hatched at the beginning of April. Head capsule width was used to determine monthly size variation and increases in growth (Tables 1 and 2). Larvae progressively increased in size from April through November. Generally, the most rapid growth occurred during the first few months of larval existence. Although larvae increased in size for most of the developmental period, no increases occurred in December or January. Therefore, larvae reached their final instar by November, overwintered in the water, and began pupating in February/March. Other studies of *Sialis* (Giani and Laville 1973, Pritchard and Leischner 1973, Woodrum and Tarter 1973, Lilly et al. 1978, Gatewood and Tarter 1983) have also found periods where larval growth slows or even stops. Woodrum and Tarter (1973) suggested this lack of growth correlated with low water temperatures. Giani and Laville's (1973) findings of *S. lutaria* with three periods of slow to no growth associated with ice cover during its 3-year life cycle supports this idea. Larval diapause has not been reported for *Sialis*, but a period of slow to no growth suggest larval diapause may occur. Chapman (1969) reported larval diapause for other holometabolous insects generally occurs in the last instar. Diapause is genetically controlled and common among the temperate insects, and is often critical to proper temporal scheduling of the life cycle, such as adult emergence (Butler 1984, Borror et al. 1989). Diapause generally occurs during adverse environmental conditions, such as reduced temperatures during winter (Chapman 1969, Butler 1984). While the water temperatures in Texas are not as cold as those of temperate streams, *Sialis* larvae in this study still exhibited this reduced growth pattern, suggesting there may be genetic constraints prohibiting early prepupal emergence. Generally, the closer an individual is to its final instar size, the more it is affected by small decreases in temperature (Ward 1992). This mechanism reduces further growth in larger sized larvae while allowing the smaller larvae to reach final instars before November/December. As a result, synchronization of adult emergence occurs in the spring, reducing the chance of emergence occurring during unfavorable conditions (Ward 1992). Adult emergence tends to be the most common point where synchronization is re-established and temperate populations tend to show greater synchrony compared to populations in the tropics (Butler 1984).

The head capsule width data (Fig. 4) indicates a univoltine life history. Many life history studies of aquatic insects find an inverse relationship between latitude and the number of generation per year (Corbet 1980, Ward and Stanford 1982, Brittain 1983, Ward 1992, Giller and Malmqvist 1998). For *Sialis*, most investigators find univoltine life histories across most of the temperate United States (Azam and Anderson 1969, Woodrum and Tarter 1973, Lilly 1976, and Lilly et al. 1978, Gatewood and Tarter 1983). However, *S. cornuta* in Canada is semivoltine (Pritchard and Leischner 1973). Studies abroad report *S. lutaria* to be univoltine (Iverson and Thorup 1987) at low latitudes and altitudes, but merovoltine at high altitudes (Giani and Laville 1973). These studies indicate temperature may affect voltinism in *Sialis* and raises the question of why *Sialis* are not bivoltine in Texas where water temperatures are warmer year-round and where larvae reach their final instar within 5 months. The geographically broad univoltine life history reported thus far across the United States, including this study in subtropical Texas, indicate *Sialis* may have genetic constraints on voltinism flexibility. Many mayflies (Ephemeroptera) also maintain a univoltine life history over a broad latitudinal range with varying temperature regimes (Sweeney et al. 1992). It appears that *Sialis* is primarily restricted to a univoltine life history, regardless of larval development and growth rates. Butler (1984) suggested that genetic constraints may mandate diapause at certain stages in order to synchronize critical life cycle events with proper environmental conditions. Environmental cues, such as seasonal temperature variations and photoperiod must be the determining factor(s) for prepupal emergence in *Sialis*. This may explain why final instars overwinter in the water and emerge during the spring. Bivoltine or merovoltine life histories reported in colder environments for *Sialis* suggests larvae simply do not grow and mature at the sufficient rate for 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.

The Town Lake and San Gabriel River populations began crawling out of the water onto the shore to pupate at different times. 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 (Fig. 5).

Feeding Habits

Of the 84 guts analyzed, 67% were empty and 33% contained food. While the number of empty guts appears high, it is not uncommon. Pritchard and Leischner (1973) found 58% of *S. cornuta* and Woodrum and Tarter (1973) 50% of *S. aequalis* had empty guts. There are several possible explanations that may account for such observations. Pritchard and Leischner (1973) found that larvae may regurgitate the gut contents when placed in a preservative solution that does not instantly kill them. To minimize regurgitation, larvae collected in this study were placed in ice cold water to shock them before they were preserved in 95% ethanol. Another possible explanation for the high percentage of empty guts is the time-of-day larvae were collected. Since *Sialis* feed at night (Chandler 1971), it is possible that prey items may be completely or partially digested by the following afternoon. Pritchard and Leischner (1973) found the rate of digestion to be dependent on temperature; the amount of time after ingestion until the first fecal pellet is produced was 106 hours at 5°C, 29 hours and 12.5°C, and 22 hours at 17.5°C. With both systems having annual mean temperatures of 20.1°C, digestion should be quite rapid. Since most larvae were collected in the afternoon, it is possible most prey items were digested. Azam and Anderson's (1969) finding that *Sialis* larvae can live up to two months without food may also explain the high percentage of empty guts in this study.

Of the 28 *Sialis* larvae (instars IV-X) with prey in the gut, only three prey taxa were found. Larval guts in Town Lake had 67% ostracods, 22% oligochaetes, and 11% chironomids, and larvae from the San Gabriel River were similar with 53% ostracods, 38% oligochaetes, and 9% chironomids. While Lilly et al. (1978) and Pritchard and Leischner (1973) found similar restricted feeding habits in *S. itasca* and *S. cornuta*, respectively, most species seem to have more diverse diets. *Sialis* larvae are generally thought to be opportunistic, feeding on the most abundant members of the benthic invertebrate community (Azam and Anderson 1969, Giani and Laville 1973, Hildrew and Townsend 1976). Prey items reported in those studies include members of the Ephemeroptera, Trichoptera, Diptera, and aquatic Acari. Gatewood and Tarter (1983) and Woodrum and Tarter (1973) reported diets high in organic detritus and filamentous algae. However, the detritus and filamentous algae may have been consumed in the process of feeding on other invertebrates or from the gut contents of prey themselves (Cummins 1979). Several (Azam and Anderson 1969, Lilly et al. 1978, Pritchard and Leischner 1973) have also reported cannibalism among *Sialis* larvae.

The most abundant potential prey for *Sialis* in this study was *Hyalella azteca* (Amphipoda) and chironomids in both Town Lake and the San Gabriel River (Tables 3 and 4). The mayfly, *Caenis* spp., was also generally abundant in the San Gabriel River (Table 3). Due to the subsampling method used, ostracods and oligochaetes, two of the three items found in the guts, are not highly represented in the habitat data. The reason *Sialis* larvae in this study did not feed on *Hyalella azteca* or *Caenis* spp. is unclear. However, Malmqvist and Giller (1998) indicated that predators are opportunistic in the sense that they eat what they can catch. It appears that *Sialis* may have a difficult time either catching or handling *H. azteca*, but Minshall (1968) did find *S. joppa* fed on *Gammarus*, another amphipod suggesting that their absence from larval guts in this study could be an artifact of sampling.

<u>Habitat Preference Experiment</u>

During collections at Town Lake, a filamentous algae suspended in the water column was found to contain *Sialis* larvae. This contradicts previous findings that *Sialis* larvae are burrowing benthic animals (Chandler 1971, Wang et al. 2001). Other studies found larvae inhabiting snag habitats (Benke et al. 1984 and Phillips 1996) but those studies reported a benthic preference for larvae. Results of the habitat preference experiment showed 3.33 (± 0.33) larvae in the sediment-only treatment and 2.00 (± 0.58) in the sediments-plus-algae treatment. Two larvae were not recovered and are presumed to have died. A paired T-test shows that when the algae is present, larvae do not prefer one habitat over the other ($p>0.11$). It is unclear why larvae were suspended in the algal mats, since they are burrowing predators. It is possible, however, that the dense algal mats allowed them to feed on invertebrates while still protecting them from predation.

Pupae

Thirty prepupae were collected in shoreline traps from 17 January 2000 through 11 April 2000 (Fig. 5). Twenty specimens collected from 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). One pupa (Fig. 12) was found at Town Lake on shore in a pupation chamber 1.5 meters from the water's edge on 31 March 2001. While pupae were not located in the field at the San Gabriel River, traps located more than eight meters from the water's edge did collect migrating prepupae. Increased temperatures are inversely related to pupation duration (Elliot 1996) and consequently should be shorter in more-southern latitudes. Duration of the pupal period was estimated to be three to four weeks based on the occurrence of the first prepupal record and the first record of adult emergence.

Adults

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. Sexual dimorphism is evident in *Sialis* with males (mean = 1.88 mm) smaller than females (mean= 2.20 mm).

Of the 73 adults collected in the field from 4 March 2001 through 11 April 2001, 62% were male and 38% female. The difference in sex ratio is likely due to differences in flying abilities between males and females. In species that do not feed as adults where sexual dimorphism occurs, female weight often exceeds male weight two-fold (Butler 1984). Since *Sialis* adults are generally weak flyers (Canterbury 1978), gravid females may not fly well. As a result, females were probably not located in the field as often. Adults were present at the San Gabriel River from 4 March 2001 through 2 April 2001. The results for Town Lake were similar with adults being present from 7 March 2001 until 11 April 2001. With the low number of *S. velata* caught in the field, it is difficult to compare emergence patterns between the two species. Whiting (1991) reported the earliest adult emergence in Texas on April 1 (Brazos County) for *S. itasca* and March 24 (Kerr County) for *S. velata*. Throughout their North American distributional ranges, Tarter et al. (1978) reported *S. itasca* with emergence periods ranging from the end of March to the end of September and from the beginning of April to the beginning of September for *S. velata*. In this study, *S. itasca* were collected at Town Lake from 4 March through 11 April and *S. velata* only on 24 March (Table 5). A similar situation occurred at the San Gabriel River where adult *S. itasca* were found from 7 March through 4 April and *S. velata* were collected only on 4 March 2001 (Table 5). At Town Lake, 7% of the males collected were *S. velata,* 93% were *S. itasca* compared to the San Gabriel River where 11% were *S. velata*, 89% *S. itasca*. There were three specimens which appeared to be intermediate between the two species. Although these specimens may represent hybrids, they more likely represent phenotypical variants of their respective parent species. A primary structure used to separate the two species, the basal lobe of the mediuncus (Fig. 20), appears to be quite variable in shape maong the adult males examined. Phenotypic variation of genitalia is somewhat characteristic of the Megaloptera. Bowles and Mathis (1992) found another megalopteran, the fishfly (*Neohermes concolor*), also exhibited wide morphological variation in genitalia.

Eggs

Sialis eggs (Fig. 10-11) collected from riparian vegetation at Town Lake ranged from 0.58-0.66 mm in length (mean=0.66), 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 caught in the field had an average of 352 eggs in their ovaries (range from 61-573). Lilly (1976) found *S. itasca* females with a mean of 539 eggs in the ovaries. The smaller number of eggs found in this study is probably a consequence of a small sample size (n=4) since field collected egg masses had an average of 525 eggs per mass (range from 145-850). Most egg masses were found on the stems of bald cypress, *Taxodium distichum*, overhanging the water. The only additional tree found bearing egg masses was box elder, *Acer negundo* (Fig. 10). Gatewood and Tarter (1983) found *S. itasca* egg masses on *Acer* spp., *Lindera benzoin*, and *Betula* sp. With the egg masses being rather difficult to locate in the field (Pritchard and Leischner 1973), determining whether *Sialis* females have a vegetation preference for ovipositing is difficult to determine.

Effects of Lentic and lotic conditions on the life history of *Sialis* spp.

Temperature and food are significant factors that regulate the life history of many aquatic insects (Ward and Stanford 1979, Brittain 1983, Butler 1984, Sweeney 1984). The temperature regimes of the respective systems in this study were temporally different, and, as a result, probably played a significant role in the growth and emergence patterns of *Sialis*. Based on the high specific heat capacity of water, seasonal temperature fluctuation in smaller bodies of water is greater than temperature fluctuations in large bodies of water. The degree-day estimate beginning in June shows the river had more net cumulative degree-days through January than the reservoir (Fig. 2). In January, the reservoir's warmer temperatures allowed it to catch up with the river's degree-days. That is, with colder ambient air temperatures, the river cools faster while the reservoir remains relatively warm. As a result, the San Gabriel River has a rapid accumulation of degree-days during the summer and a reduced accumulation during the winter. In contrast, Town Lake's less variable temperatures in the summer and winter allow a somewhat steady accumulation of degree-days. As a consequence of the warmer river water in the summer, larval growth was more rapid (Figs. 4 and 7). Most larvae in the San Gabriel River were in their 10th instar by August, just five months after hatching. With maturation occurring so early, a bivoltine life history in this river appeared possible. A fall emergence, however, did not occur. As mentioned previously, a spring adult emergence may be genetically fixed. *Sialis* mainly occur in temperate regions and it is likely they evolved in habitats with distinct seasonal patterns, as opposed to the subtropical regions where seasonal patterns are less defined. Adult emergence in temperate regions is thought to occur during the spring when optimal conditions exist for young instars (Butler 1984, Huryn and Wallace 2000). If adults were to emerge in the fall and hatching take place before winter, prey size may be problematic for young instars in temperate regions. In the southern latitudes, however, seasonal patterns are not as defined and as a consequence, multivoltine and asynchronous life histories are typically found (Tiemann and Arsuffi 1991). It appears, therefore, that the evolution of *Sialis* in temperate regions prevents a bivoltine life history in southern latitudes.

In addition to the faster growth rates in the lotic system, prepupal emergence patterns were earlier for the river populations. Prepupae in the river had an emergence period from mid-January to the end of January. In contrast, Town Lake prepupae did not begin emerging until the beginning of March and lasted through mid-April. Photoperiod is thought to be a major environmental cue for emergence patterns (Butler 1984, Nylin et al. 1996). However, with the six-week difference between the first prepupa emerging in the river and the reservoir, it appears additional environmental cues (probably temperature) are involved.

Various aspects of nutrition are usually studied when examining life histories (Butler 1984). Prey found in the river and reservoir were similar (Tables 3 and 4), as were prey composition in the guts of river and reservoir larvae. Although prey size was not measured, all taxa were assumed to be potential prey for *Sialis* at some stage in their life cycle. The lack of detectable feeding differences in the two systems suggest food quality is not responsible for the rapid growth and large larval sizes in the river. Instead, temperatures appear to be associated with rapid growth in *Sialis*.

Resource Partitioning: *Sialis itasca* and *Sialis velata*

It was thought from previous historical collections that only *Sialis velata* occurred in Town Lake. Until this study, no specimens of *S. itasca* were collected at the present study sites. The discovery of two congeneric species of *Sialis* coexisting in both Town Lake and the San Gabriel River raises questions concerning interspecific competition for environmental resources. It is uncommon to find two closely-related species of predatory insects inhabiting the same habitat (Sweeney and Vannote 1981). Collection records nationwide, however, indicate an overlapping range where both species coexist in the same streams and habitats. According to the Competitive Exclusion Principle, however, no two species can coexist indefinitely in the same habitat on the same environmental resources (Hardin 1960, Schoener 1974). Interspecific competition is thought to drive one species to extinction or create a spatial or temporal separation in life history characteristics (Cummins 1979) such as developmental timing, feeding habits, and emergence patterns. The staggering of life cycles of coexisting species of Ephemeroptera, Plecoptera, and Trichoptera serves as a mechanism to reduce competition among larvae (Minshall 1968, Sweeney and Vannote 1981, Brittain 1983). Ross (1937) suggested that different seasonal adjustments in adult emergence patterns for coexisting populations of *S. itasca* and *S. velata* explained the coexistence he found. Too few adults were collected of *S. velata* to determine if staggering emergence patterns could play a role in reducing overlap. If, however, adults of both species emerge at the same time, the closely related larvae must be partitioning their habitats at some level not determined in this study. Since species identification of the larval stage is currently not feasible, different microhabitat-utilization patterns of larvae cannot be detected. If no partitioning is taking place, the Competitive Exclusion Principle predicts the eventual extinction of one species. With the small percentage (9%) of *S. velata* being found compared to *S. itasca* (91%), it is possible an extinction may be taking place. However, since this study provided a snapshot of one generation occurring at both locations, it is impossible to determine without long-term historical data. The coexistence of the two species at both Town Lake and the San Gabriel River should be investigated over the next several generations to determine if competition is actually occurring.

A Key to adult male *Sialis* occurring or possibly occurring in Texas

The following key of seven species found in Texas or in neighboring states (Fig. 15) is provided for two reasons. First, there are many larval records of the genus in Texas, but the actual species are unknown. It is likely some of the species occurring in Louisana, Arkansas, and Oklahoma occur in Texas as well. Also, it should be noted the two species of the current study, *S. itasca* and *S. velata* are sister species (Whiting 1994) and therefore can be easily misidentified. The shape of the basal lobe of the mediuncus is a primary characteristic used to separate the two species (Ross 1937) but is highly variable. Therefore, additional characters are provided for *S. itasca* and *S. velata*.

1a. Ninth sternite produced into a flap covering most of the genitalia (Fig. 16A)..*Sialis vagans* Ross

1b. Ninth sternite not produced into a flap (Fig. 16A-18B)...(2)

2a. Ectoproct produced at apex into a pair of long arms (Fig. 19B)..*Sialis mohri* Ross

2b. Ectoproct sometimes with an apical incision (Fig. 20A) or a pair of short "horns," but not with a pair of long arms...(3)

3a. Legs with femora rufous and tibiae the same color or blackish; head with distinct red/orange bands extending to pronotum; genitalia as in Fig. 17A........... *Sialis americana* (Rambur)

3b. Legs black, or with tibiae slightly lighter than femora; head black..(4)

4a. Mediuncus long and whiplike (Fig. 19B-20B)
extending forward between the parameres
(Fig. 17B-18B)..(5)

4b. Mediuncus short, never longer than the gonarcus
from which they arise (Fig. 19B); parameres always
closely appressed on meson (Fig. 16B)......................................*Sialis joppa* Ross

5a. Apex of parameres produced into large knobs (Fig. 17B)......*Sialis infumata* Newman

5b. Apex of parameres not knoblike..(6)

6a. Basal lobe of mediuncus small, ectoproct as long as
mediuncus is high (Fig. 20A); parameres broadly
rounded posteriorly...*Sialis velata* Ross

6b. Basal lobe of mediuncus markedly robust compared
with distal lobe; ectoproct shorter than mediunci are
high (Fig. 20B); parameres tapering posteriorly.........................*Sialis itasca* Ross

SUMMARY AND CONCLUSIONS

The life history of *Sialis* spp. was studied in a lentic and lotic ecosystem in central Texas. Two species, *Sialis velata* and *Sialis itasca,* were found to inhabit both systems, and both are widespread across North America. The life history of *S. velata* is unknown and Lilly (1978) provided the life history of *S. itasca* in West Virginia.

Sialis in central Texas is univoltine and has 10 larval instars. Larvae are present from April through January. First instar head capsule widths range from 0.30 - 0.35 mm. The greatest growth occurs in the early summer for larvae in the San Gabriel River and late summer for larvae in Town Lake. The San Gabriel River's cohort size range was less than that of Town Lake. Larvae in both systems reached their final instar by November, overwintered in the water, and began pupating in the spring. Prey consisted of ostracods, oligochaetes, and chironomids at both sites.

Prepupal emergence patterns differed in the two systems studied. At the San Gabriel River, prepupae were collected between mid-January through the end of January. Town Lake prepupae were not collected until the beginning of March, ending in mid-April.

Adults were present from the beginning of March until mid-April at both sites. Females oviposited on the stems and leaves of the bald cypress, *Taxodium distichium*, and the box elder, *Acer negundo,* overhanging the water at Town Lake. Egg masses consisted of an average of 525 eggs/mass.

The different effects of lentic and lotic conditions on *Sialis* in central Texas appear to be minimal and temperature-related. Larval growth was rapid in the San Gabriel River where temperatures were warmer. During the cooler months when the reservoir was warmer than the river, larval size in Town Lake caught up with those in the river. Prepupal emergence patterns were also affected. The San Gabriel River prepupal emergence occurred in January, while Town Lake prepupae didn't emerge until March. Photoperiod, therefore, is not solely responsible for prepupal emergence. Temperature regimes, perhaps interacting with photoperiod, are probably cues for prepupal emergence.

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Table 1. Monthly growth - head capsule width (± SD) of *Sialis* collected from the San Gabriel River from May 2000 through September 2001.

Month	N	Mean Head Capsule Width (mm) (± SD)	Range Head Capsule Width (mm)	Increase in Growth (%)
May	36	1.28 (± 0.28)	0.75 - 1.80	
June	33	1.46 (± 0.25)	0.95 - 2.37	14
July	12	1.74 (± 0.30)	1.20 - 2.37	19
August	47	1.79 (± 0.35)	1.20 - 2.35	3
September	34	1.91 (± 0.25)	1.53 - 2.50	7
October	53	1.97 (± 0.35)	1.15 - 2.67	3
November	8	2.41 (± 0.33)	2.00 - 2.80	22
December	15	2.29 (± 0.29)	1.87 - 2.90	-5
January	2	1.97 (± 0.09)	1.90 - 2.03	-14
February	none			
March	none			
April	2	0.37 (± 0.09)	0.30 - 0.44	
May	24	1.00 (± 0.25)	0.52 - 1.65	170
June	36	1.48 (± 0.23)	1.11 - 1.98	48
July	48	1.66 (± 0.29)	1.20 - 2.34	12
August	27	1.73 (± 0.21)	1.28 - 2.07	4
September	8	1.84 (± 0.22)	1.50 - 2.06	6

Table 2. Monthly growth - head capsule width (± SD) of *Sialis* collected from Town Lake from May 2000 through September 2001.

Month	N	Mean Head Capsule Width (mm) (± SD)	Range Head Capsule Width (mm)	Increase in Growth (%)
May	11	0.80 (± 0.81)	0.30 - 1.25	
June	205	0.95 (± 0.35)	0.41 - 2.25	19
July	22	0.97 (± 0.29)	0.62 - 1.76	2
August	28	1.29 (± 0.40)	0.84 - 2.33	33
September	9	1.63 (± 0.42)	1.03 - 2.45	26
October	10	1.77 (± 0.43)	1.30 - 2.77	9
November	7	2.13 (± 0.33)	1.71 - 2.80	20
December	2	2.13 (± 0.52)	1.76 - 2.50	0
January	8	2.05 (± 0.23)	1.78 - 2.39	-4
February	none			
March	none			
April	4	0.79 (± 0.17)	0.66 - 1.04	
May	123	0.89 (± 0.29)	0.37 - 1.96	13
June	175	1.15 (± 0.37)	0.57 - 2.25	29
July	160	1.23 (± 0.38)	0.65 - 2.41	7
August	40	1.46 (± 0.30)	1.02 - 2.22	19
September	9	1.50 (± 0.42)	0.99 - 2.08	3

Table 3. Taxonomic composition of available invertebrate prey for *Sialis* larvae in the San Gabriel River. Numbers indicate the percentage of possible prey collected on each sampling date.

Taxon	Jan 17	May 25	June 13	July 25	Aug 10	Sept 13	Oct 06	Nov 17	Dec 20
n=	76	139	93	88	162	96	37	91	84
Ephemeroptera									
Ephemeridae									
Hexagenia	1.3	----	2.2	1 1	----	----	----	2.2	----
Caenidae									
Caenis	6 6	12 9	6.5	26 1	13.0	28 1	13 5	1.1	1 2
Baetidae	----	3.6	3 2	5.7	3.1	2 1	18 9	----	2 4
Heptageniidae									
Stenonema	1.3	0 7	----	1.1	1 2	----	----	----	----
Tricorythidae									
Leptohyphes	1 3	2.2	1 1	----	2 4	----	----	1.1	----
Tricorythodes	----	2 2	----	----	0 6	9 4	----	----	----
Coleoptera									
Elmidae									
Dubiraphia	----	19.4	9.6	2.3	4 9	----	----	6.6	2 4
Neoelmis	----	----	7.5	8 0	----	----	----	4 4	----
Macrelmis	----	----	----	----	----	----	2.7	----	----
Haliplidae									
Peltodytes	----	----	----	----	1.2	1 0	----	----	----
Hydrophilidae									
Berosus	1 3	2.9	7 5	2.3	----	3.1	----	6 6	15.4
Trichoptera									
Glossosomatidae									
Protoptila	----	----	1 1	----	----	----	----	----	----

Table 3. -(continued)

Taxon	Jan 17	May 25	June 13	July 25	Aug 10	Sept 13	Oct 06	Nov 17	Dec 20
n=	76	139	93	88	162	96	37	91	84
Odonata									
Coenagrionidae									
Argia	----	2.2	----	1 1	----	----	----	5.5	1 2
Coenagrion	1.3	1 4	1 1	----	----	----	----	2 2	7.1
Ischnura	----	----	----	----	----	----	----	----	4.8
Gomphidae									
Styrulus	----	0 7	----	----	----	----	----	----	----
Gomphus	----	----	----	----	----	1 0	----	----	----
Corduliidae									
Macromia	----	----	----	----	----	----	2.7	2.2	----
Aeshnidae									
Basiaeschna	----	----	----	----	----	----	----	1 1	----
Anax	----	----	----	----	----	----	----	----	2 4
Libellulidae									
Libellula	----	----	----	----	----	----	----	1 1	----
Diptera									
Chironomidae	69 9	32.5	20 4	35.2	22 4	25 1	32.4	19 7	13 1
Ceratopogonidae									
Mallochohelea	----	1.4	----	----	----	----	5 5	----	----
Probezzia	----	----	----	----	----	----	2.7	----	----
Dasyhelea	----	----	----	----	----	----	2 7	----	----
Monohelea	----	----	----	----	1.2	1.0	----	----	----
Pelecypoda									
Sphaeriidae	----	4 3	4 3	8 0	----	----	----	1 1	----
Amphipoda									
Hyallelidae									
Hyalella azteca	11.8	12 9	34.4	3 4	41.4	24 0	8 1	30.8	46.4

Table 3. -(continued)

Taxon		Jan 17	May 25	June 13	July 25	Aug 10	Sept 13	Oct 06	Nov 17	Dec 20
	n=	76	139	93	88	162	96	37	91	84
Hirudinea		----	0.7	----	----	----	2.1	----	1 1	----
Oligochaeta		3 9	----	1.1	5.7	8 6	3 1	8 1	12.1	3 6
Ostracoda		1 3	----	----	----	----	----	2.7	1 1	----

Table 4. Taxonomic composition of available invertebrate prey for *Sialis* larvae in Town Lake. Numbers indicate the percentage of possible prey collected on each sampling date.

Taxon		Jan 17	Apr 19	May 20	June 13	July 25	Aug 24	Sept 23	Oct 20	Nov 17
	n=	91	93	88	92	104	103	99	91	99
Ephemeroptera										
Caenidae										
Caenis		1.1	1.1	2.3	----	----	----	----	1.1	1.0
Baetidae		1.1	----	----	----	13.7	----	4.0	2.2	4.0
Heptageniidae										
Stenonema		----	----	----	1.1	1.0	2.9	1.0	----	----
Tricorythidae										
Leptohyphes		----	----	----	----	1.0	----	----	----	----
Tricorythodes		----	----	----	----	1.0	1.9	----	----	----
Coleoptera										
Elmidae										
Dubiraphia		7.6	----	1.1	1.1	1.0	3.9	----	----	2.0
Haliplidae										
Peltodytes		----	2.2	1.1	3.3	4.8	1.9	----	1.1	----
Lutrochidae										
Lutrochus		----	----	----	----	1.0	----	----	----	----
Hydrophilidae										
Berosus		----	----	----	----	----	----	----	----	2.0
Trichoptera										
Polycentropodidae										
Cernotina		----	----	----	----	----	----	1.0	----	----
Hydropychidae										
Smicridea		1.1	----	----	----	----	----	----	----	----

Table 4. --(continued)

Taxon	Jan 17	Apr 19	May 20	June 13	July 25	Aug 24	Sept 23	Oct 20	Nov 17
n=	91	93	88	92	104	103	99	91	99
Odonata									
Coenagrionidae									
Argia	----	----	1 1	1 1	----	----	1 0	----	----
Coenagrion	----	----	----	----	----	1 0	----	2 2	----
Diptera									
Chironomidae	38 4	39 6	8 0	9.6	1.0	26 2	12 1	12.1	13 1
Lepidoptera									
Pyralidae									
Petrophila	----	----	----	----	----	----	----	1 1	----
Pelecypoda									
Sphaeriidae	1.1	1 1	----	----	----	----	----	----	----
Decapoda									
Palaemonidae									
Palaemonetes	----	----	----	----	4.8	1.0	----	4 4	3 0
Amphipoda									
Hyallelidae									
Hyalella azteca	44 0	45 2	76 1	77.9	64 9	36 0	71.8	75 8	68 9
Hirudinea	1 1	1 1	2.3	1.1	----	1.0	1 0	----	1.0
Oligochaeta	3 3	8.6	5.7	4.8	----	21 3	8 1	----	1.0
Ostracoda	2.2	1 1	2 3	----	5 8	2.9	----	----	4.0

Table 5. Distribution of adult *Sialis itasca* and *S. velata* in the San Gabriel River and Town Lake. Adult males were identified to species, females presently cannot be distinguished to species.

Date	*Sialis itasca*	*Sialis velata*	Females
SAN GABRIEL RIVER			
4 March 2001	3	2	5
20 March 2001			1
2 April 2001	11		1
4 April 2001	1		
TOTAL:	**16**	**2**	**7**
TOWN LAKE			
4 March 2001			1
7 March 2001	5		3
17 March 2001	1		2
24 March 2001	13	2	7
4 April 2001	5		8
11 April 2001	2		1
TOTAL:	**26**	**2**	**22**

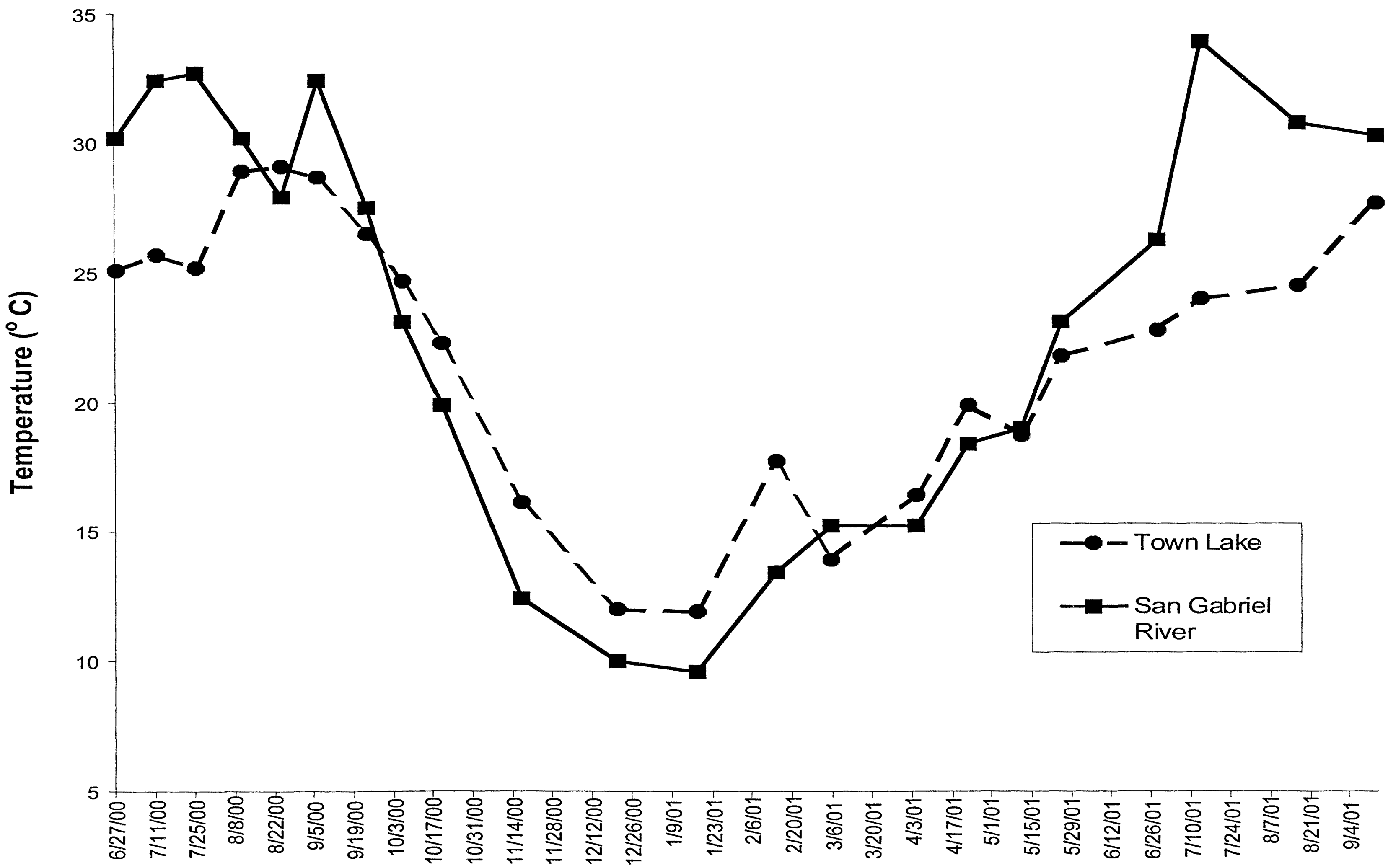


Figure 1. Seasonal temperature patterns in Town Lake and the San Gabriel River.

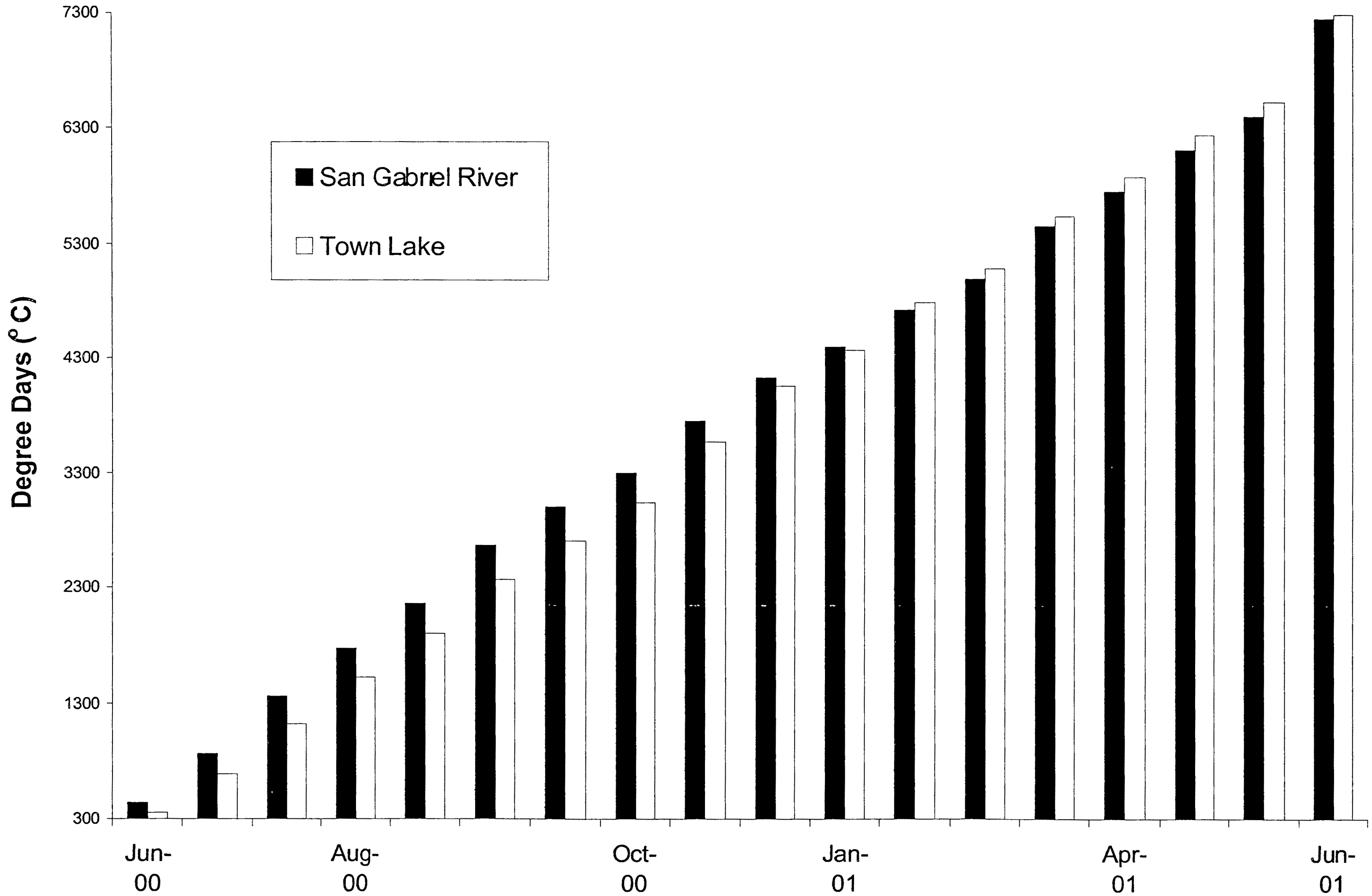


Figure 2. Cumulative degree days for Town Lake and the San Gabriel River.

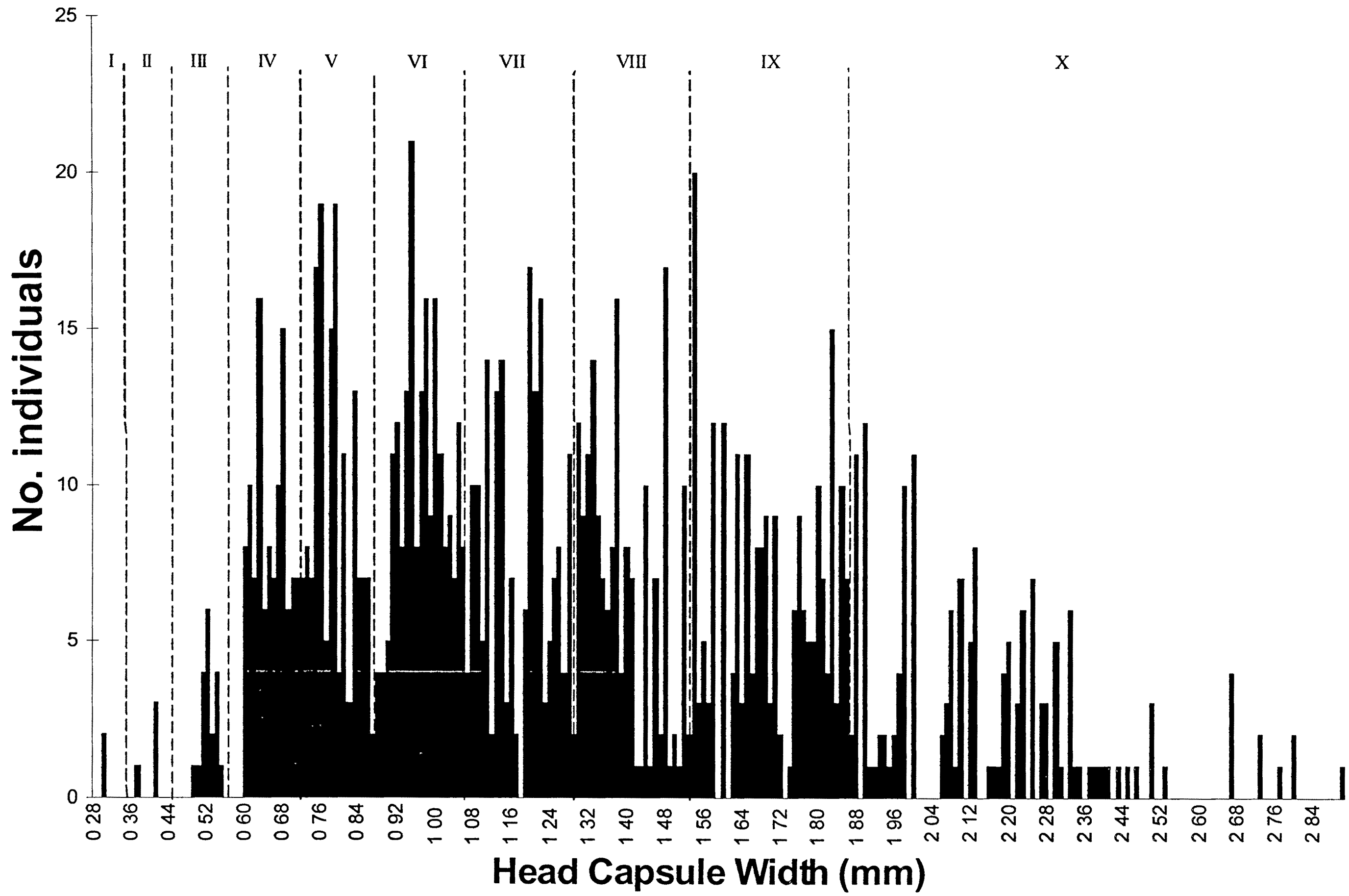


Figure 3. Distribution of larval head capsule widths of *Sialis* spp. collected in Town Lake and the San Gabriel River. Roman numerals and dashed lines indicate the approximate instar size ranges.

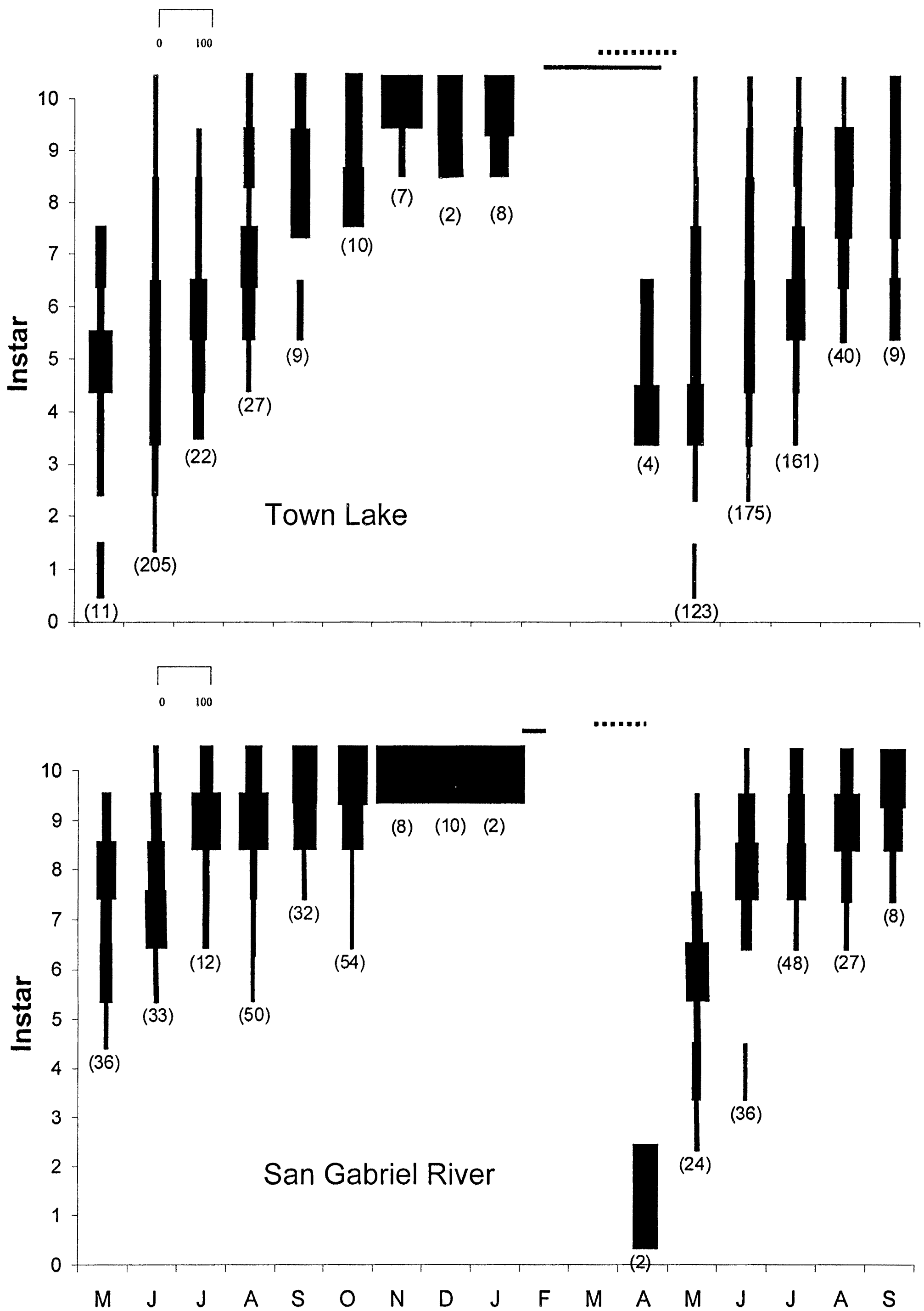


Figure 4. Life history of *Sialis* spp. in Town Lake and the San Gabriel River. The width of each bar represents the percentage of each instar collected and numbers under the bars indicate the number of larvae collected that month. Solid lines above the bars indicate the month(s) when prepupae were trapped; dashed lines above the bars indicate when adults were collected.

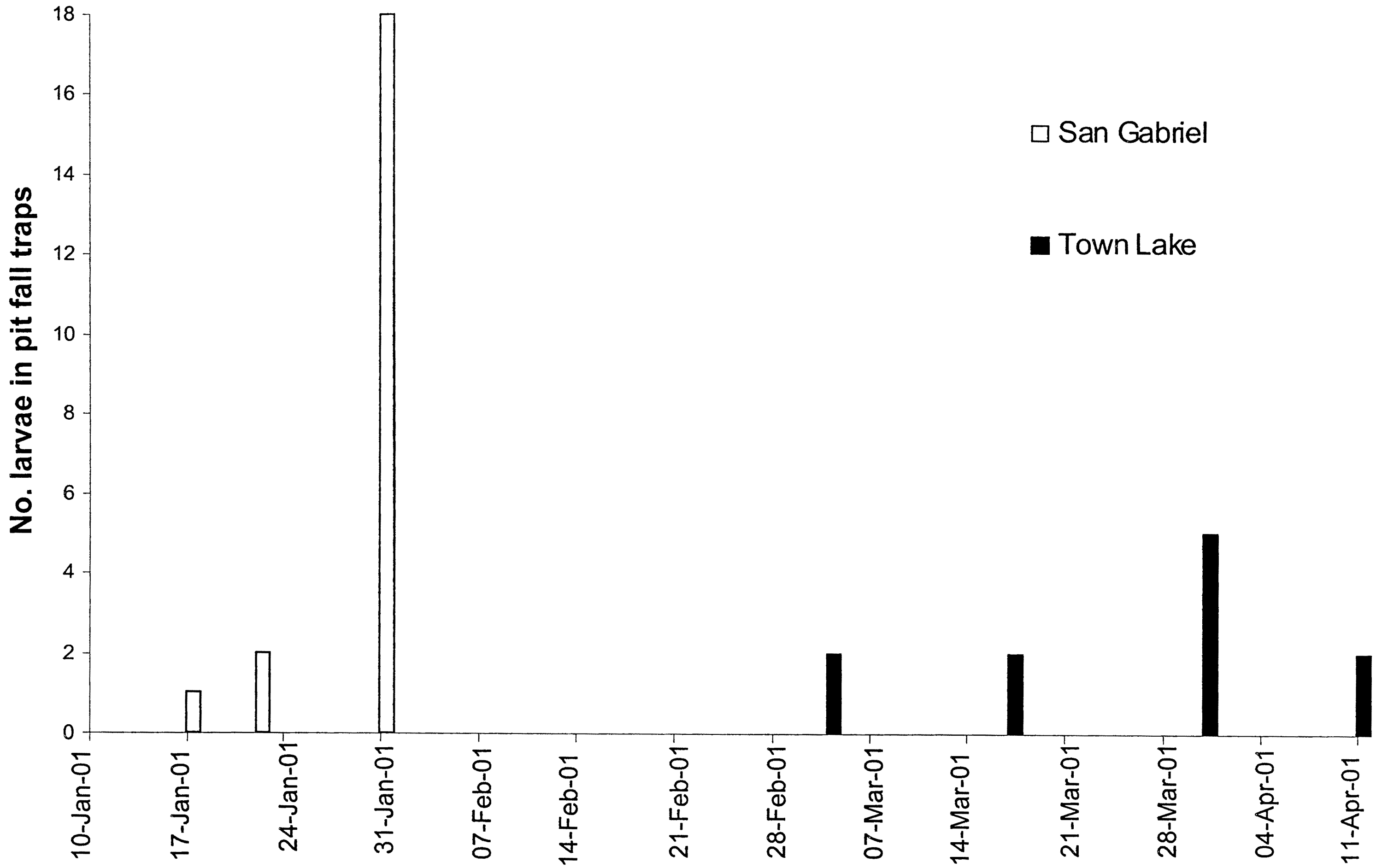


Figure 5. Prepupal emergence patterns of *Sialis* spp. at Town Lake and the San Gabriel River.

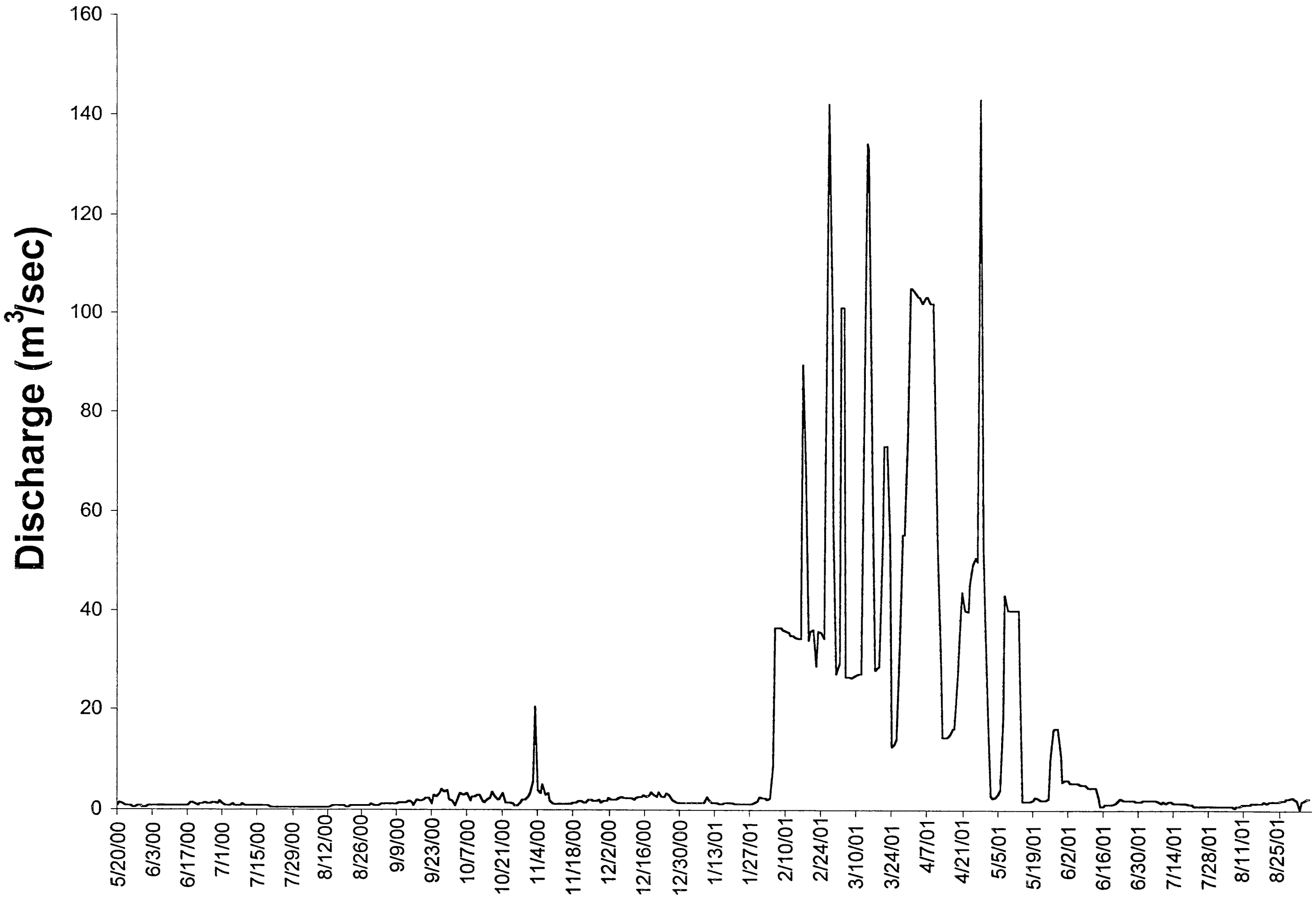


Figure 6. Discharge in the San Gabriel River during the study. Data from USGS station 08104700.

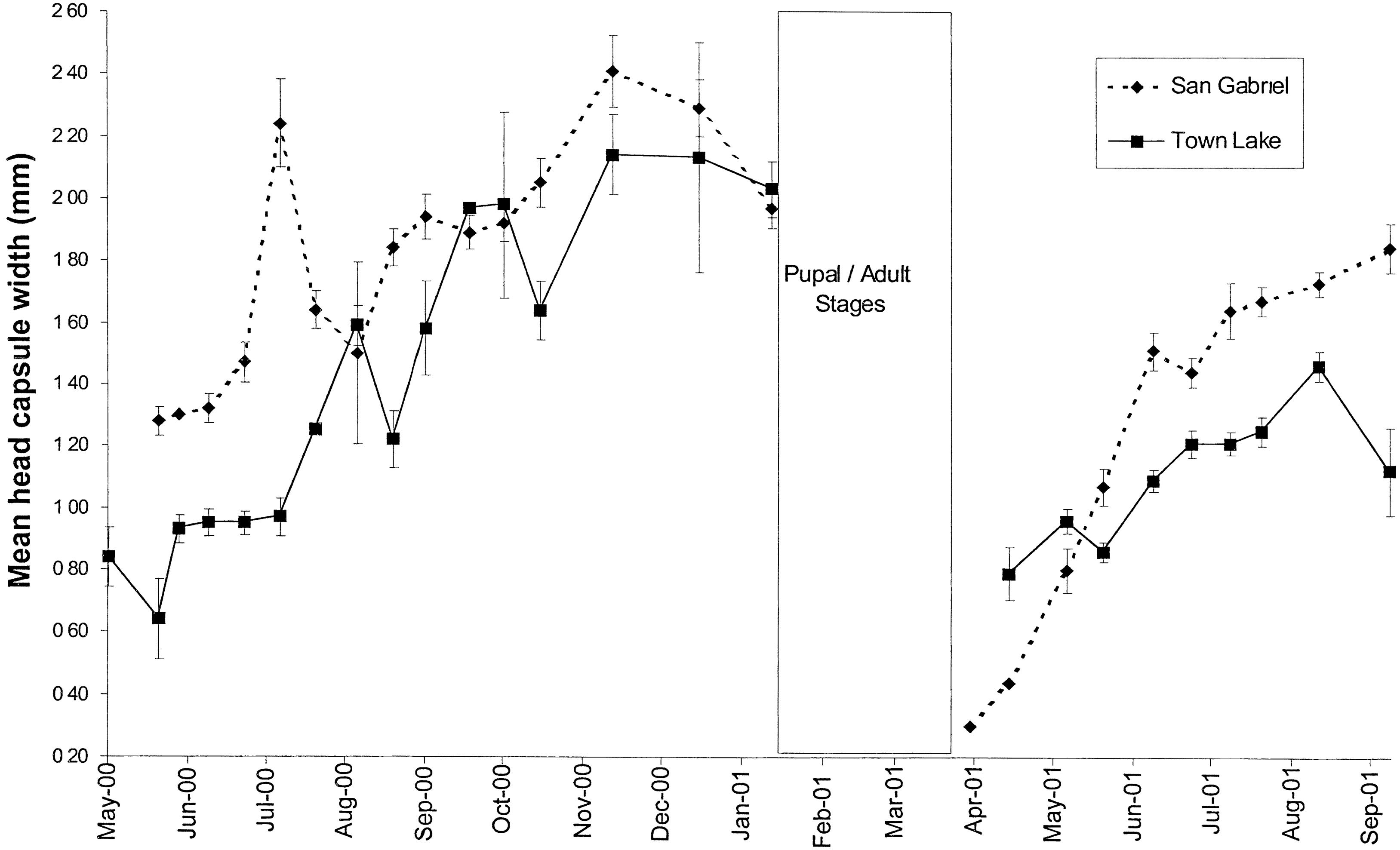
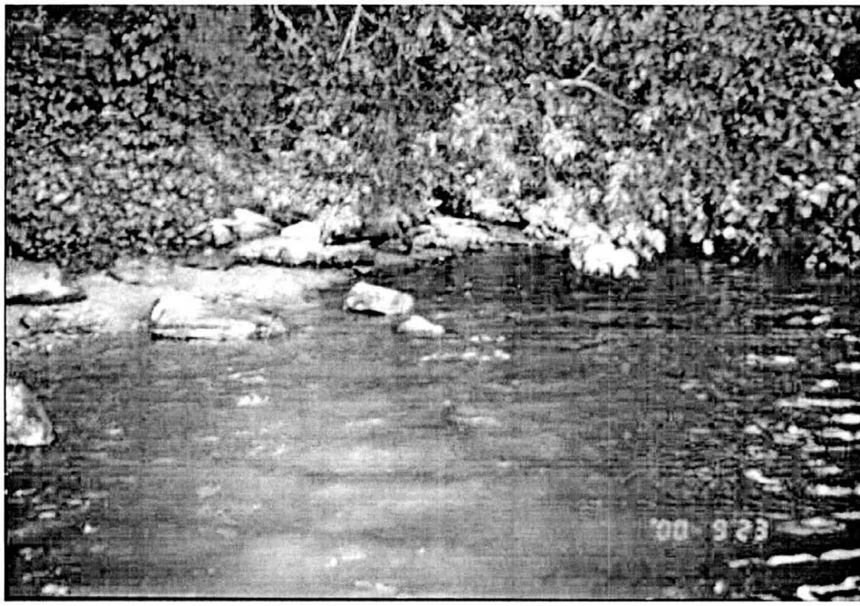


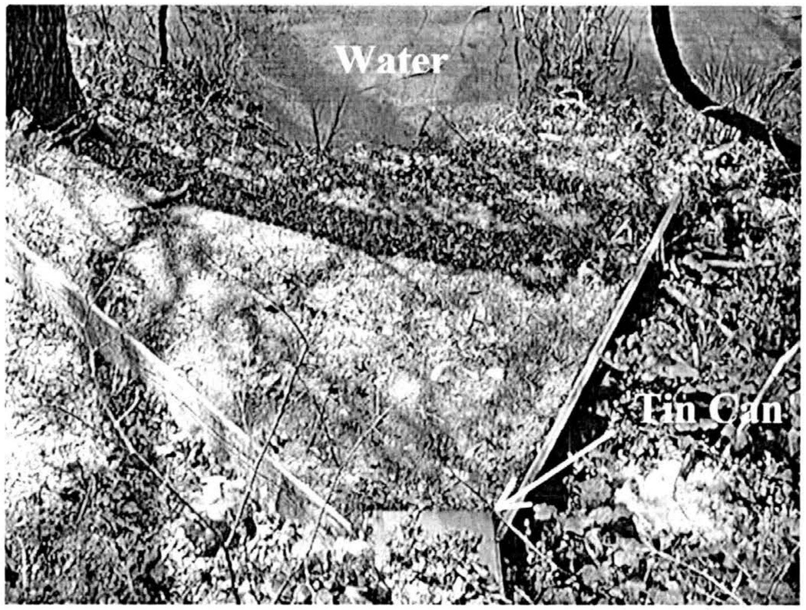
Figure 7. Mean monthly head capsule (± 1 SE) width in *Sialis* spp. larvae at Town Lake and the San Gabriel River..



A

B

Figure 8. Collection sites of *Sialis* at Town Lake (A) and the San Gabriel River (B).



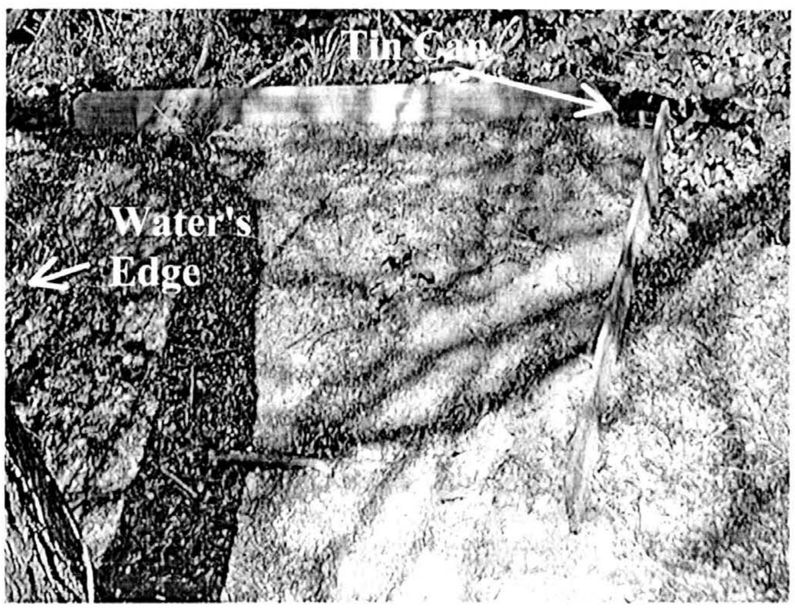


Figure 9. Terrestrial prepupal traps oriented perpendicular to the water on the shore of Town Lake. Prepupae were trapped in a tin can at the apex.

A

B

Figure 10. Egg masses collected at Town Lake on the underside of a Box Elder (*Acer negundo*) leaf (A) and along the stems (B).

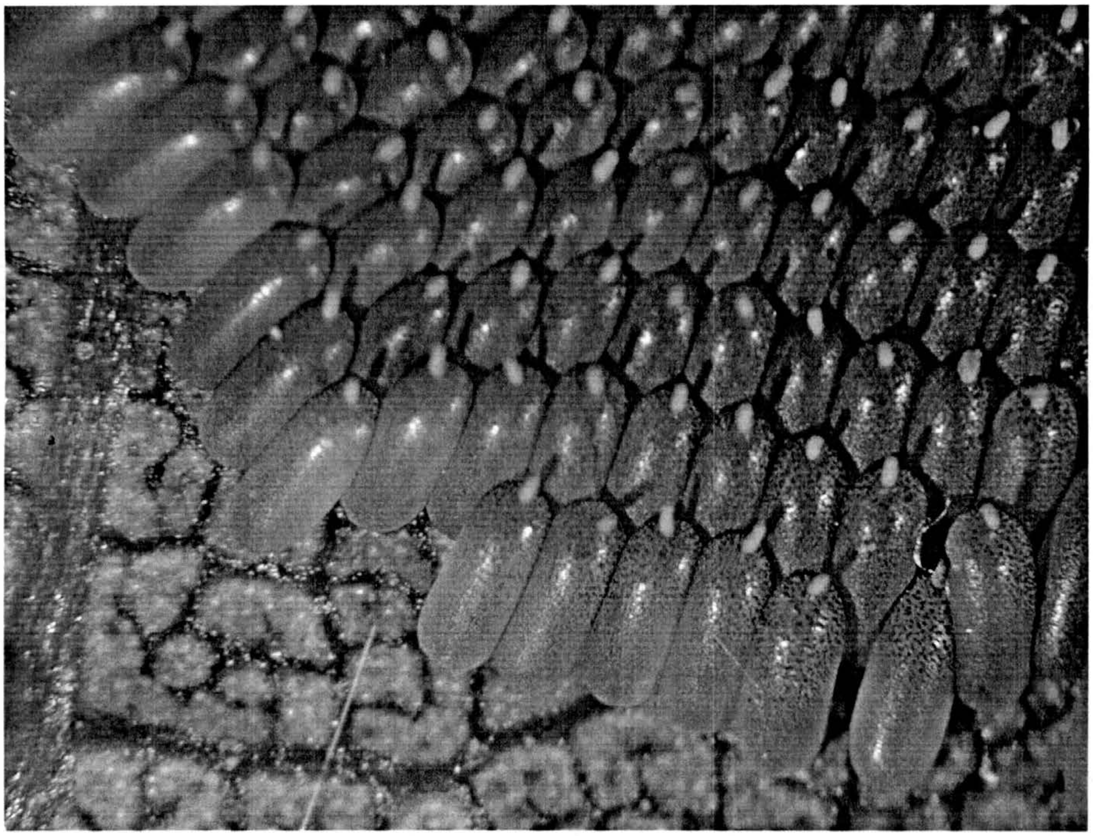
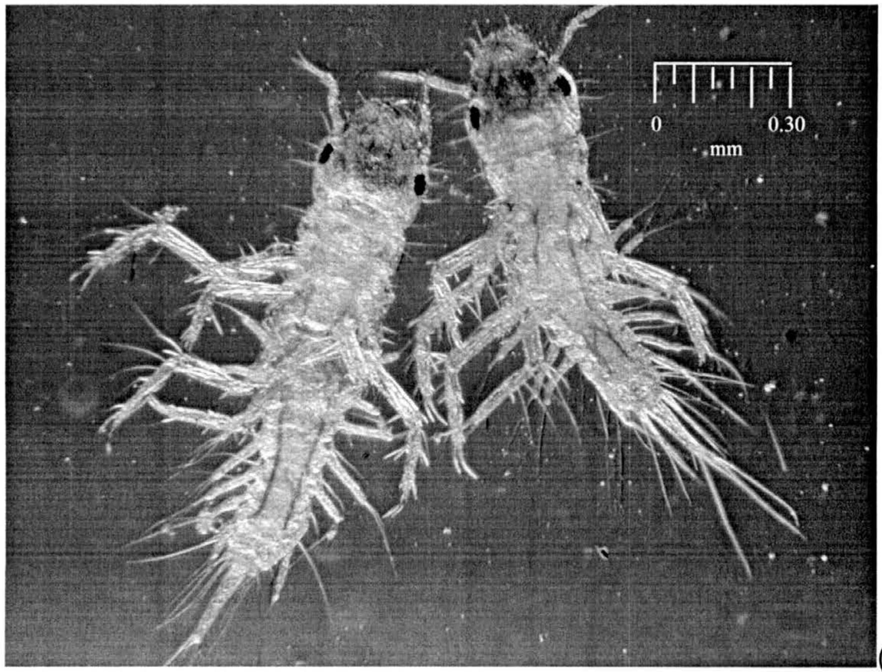


Figure 11. Eggs of *Sialis* on the bottom side of the Box Elder leaf



(A)

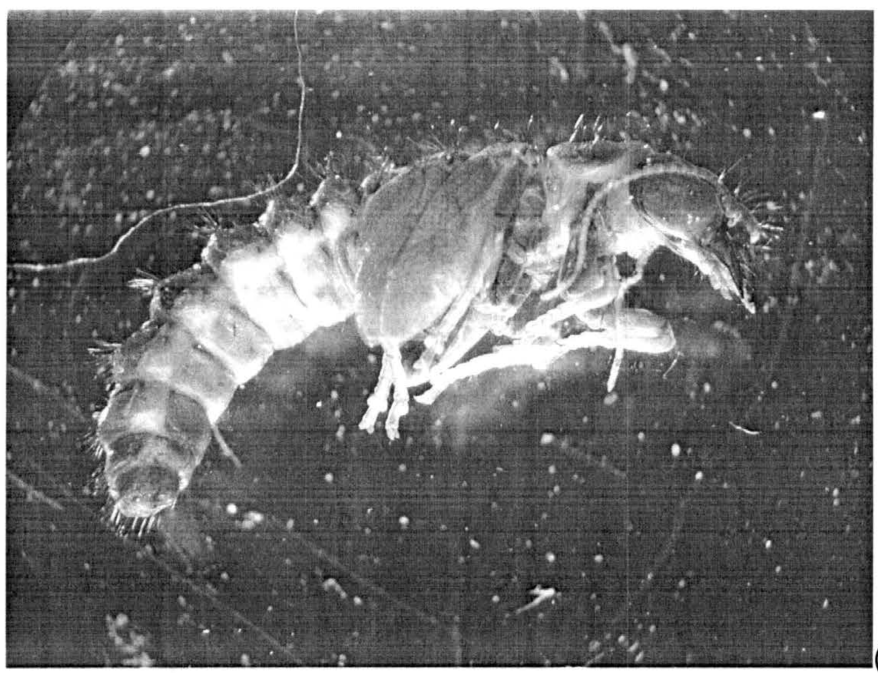

(B)

Figure 12. First instar *Sialis* larvae reared from eggs collected at Town Lake (A) and pupa collected in pupation chamber on the shore of Town Lake (B).

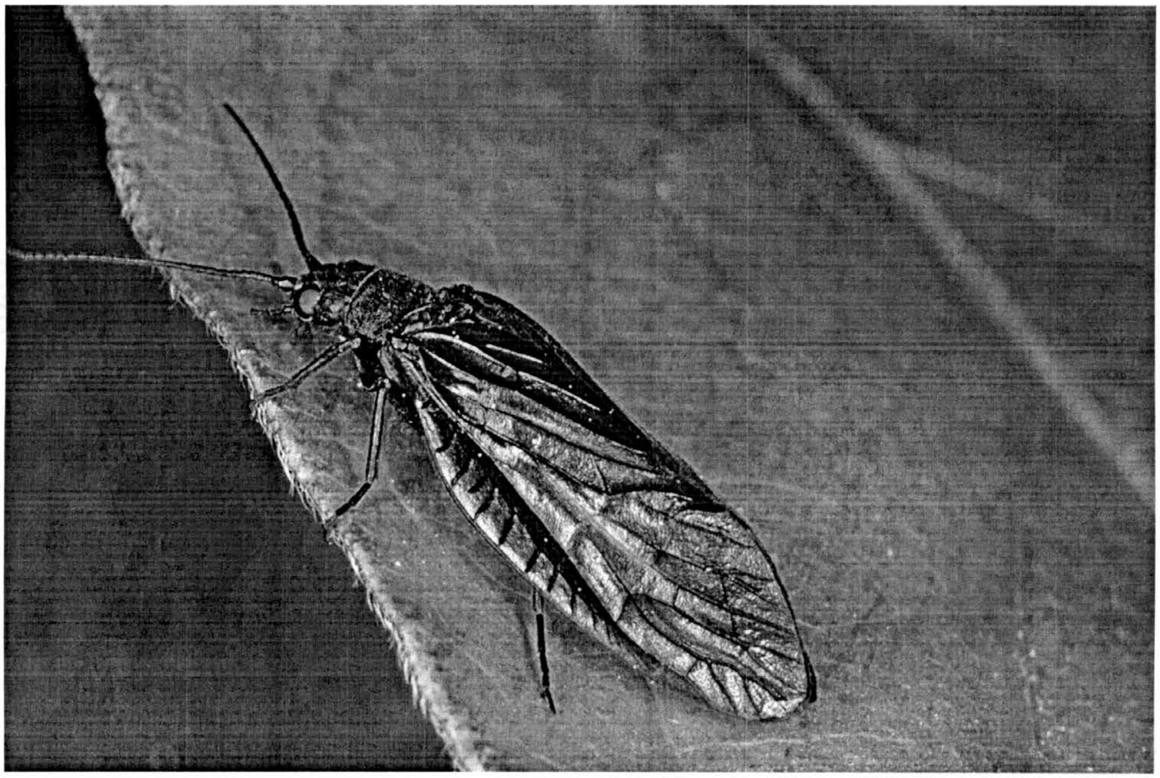


Figure 13. Adult *Sialis* collected at Town Lake.

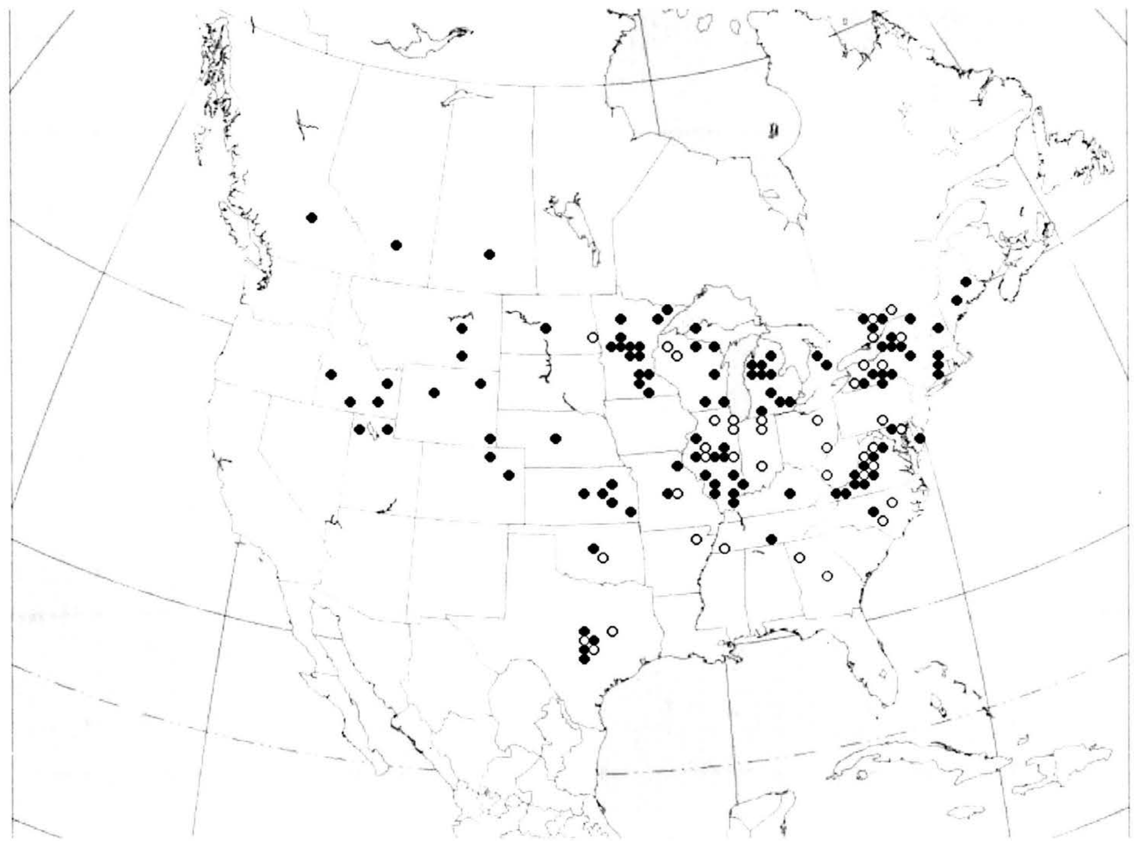


Figure 14. Distributional ranges of *Sialis itasca* (open circles) and *Sialis velata* (closed circles) in the North America. Records from Whiting (1991).

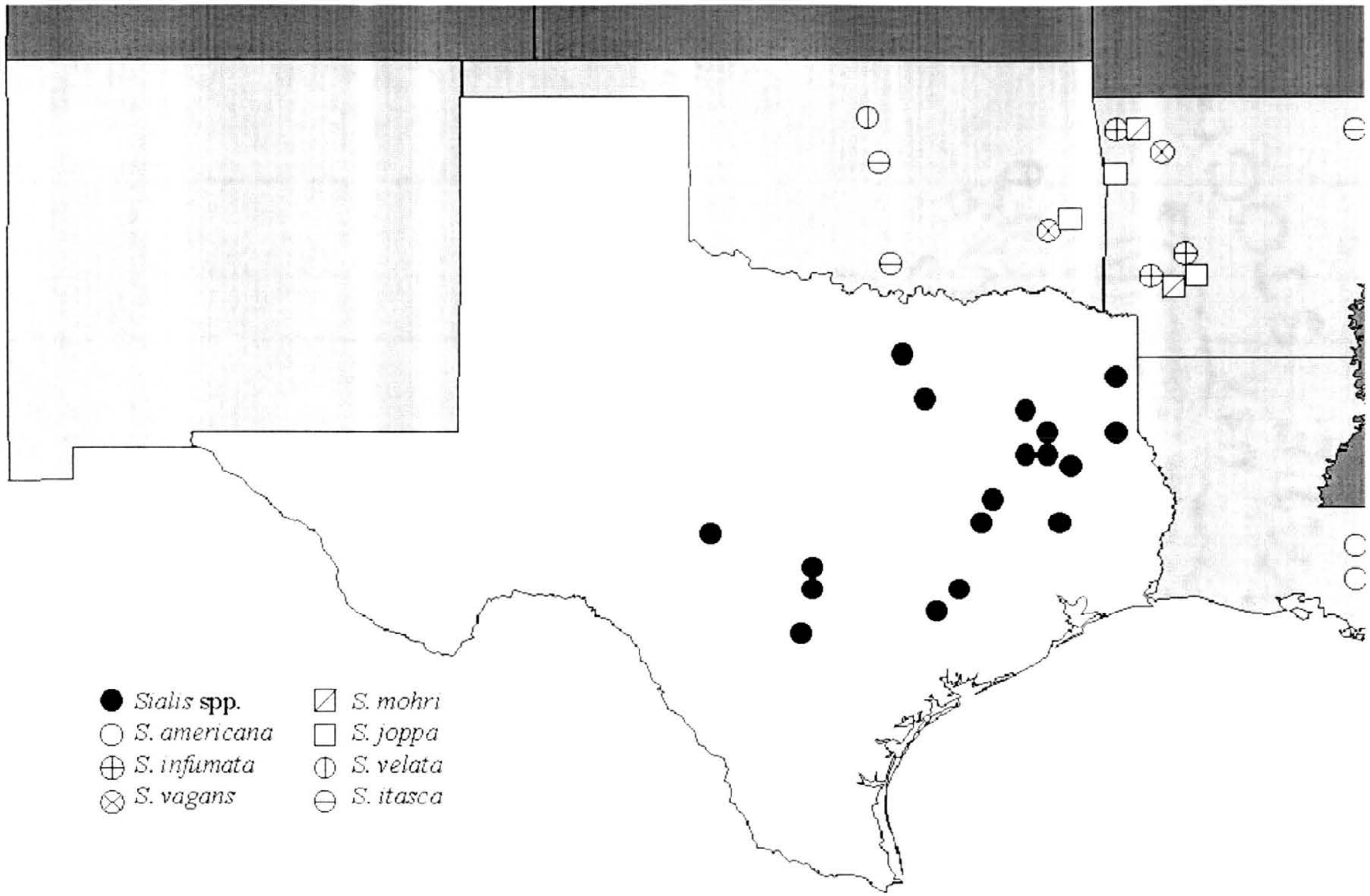
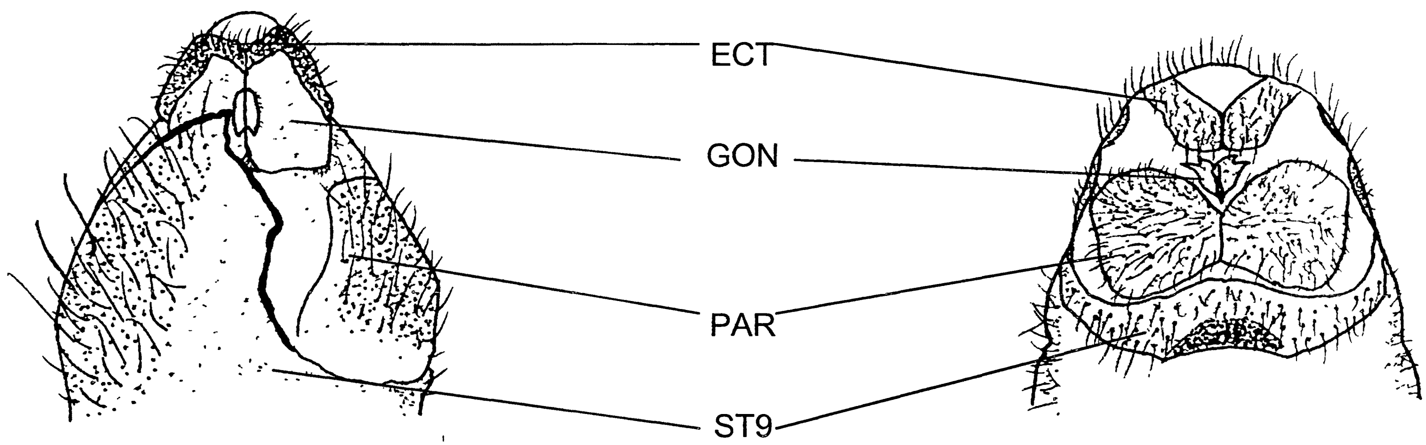


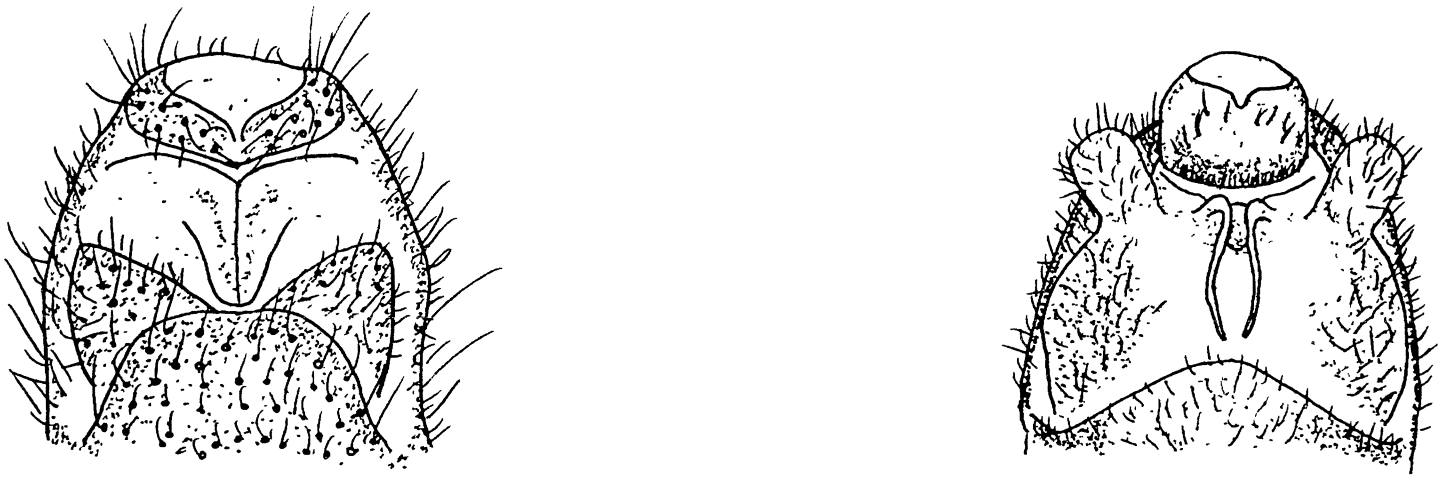
Figure 15. Known distributions of *Sialis* larvae in Texas and the distributions of species occurring in neighboring states. Adult records from Whiting (1991) and larval records from the collections of Dr. David Bowles.



A
Sialis vagans

B
Sialis joppa

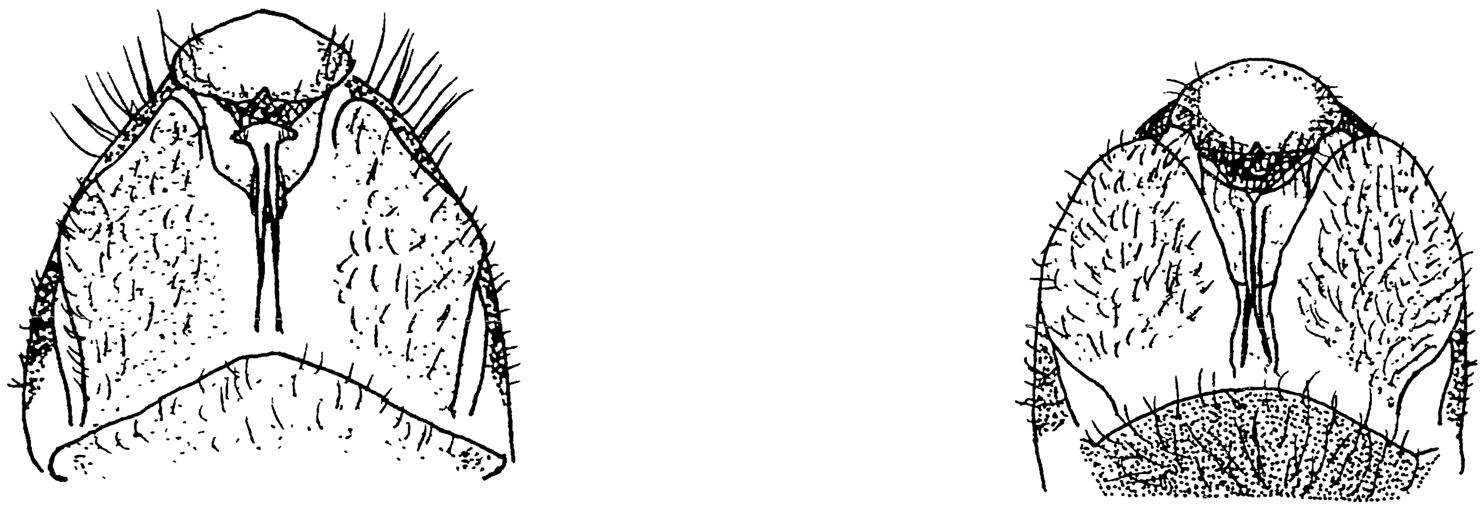
Figure 16. Ventral view of *S. vagans* (A) and *S. joppa* (B) male genitalia. Abbreviations: ECT, ectoprocts; GON, gonarcus; PAR, parameres; ST9, sternum 9.



A
Sialis americana

B
Sialis infumata

Figure 17. Ventral view of *S. americana* (A) and *S. infumata* (B) male genitalia.



A
Sialis itasca

B
Sialis velata

Figure 18. Ventral view of *S. itasca* (A) and *S. velata* (A) male genitalia.

(a) (b)

A
Sialis joppa

(a) (b)

B
Sialis mohri

Figure 19. Lateral (a) and caudal (b) view of *S. joppa* (A) and *S. mohri* (B) male genitalia.

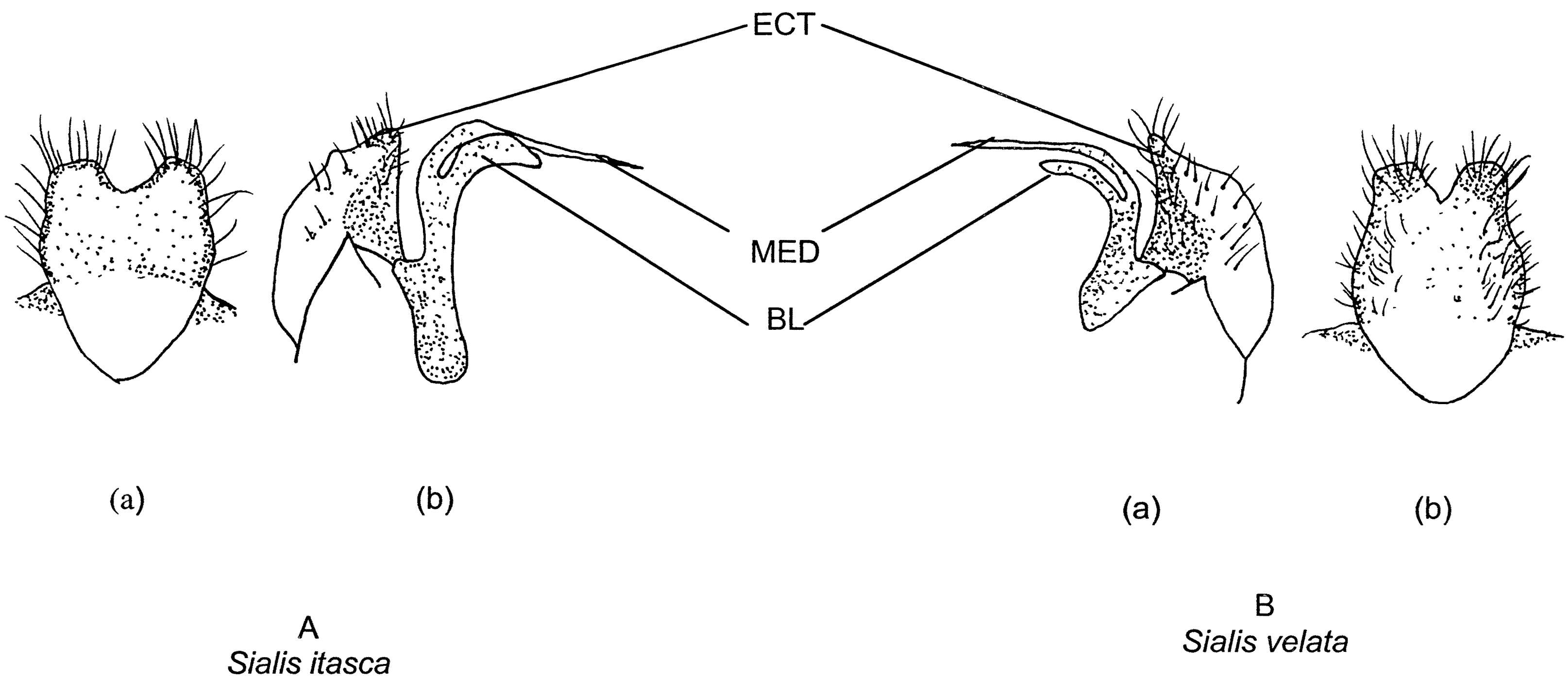


Figure 20. Caudal view (a) (ectoproct) and lateral (b) view of *S. itasca* (A) and *S. velata* (B) male genitalia. Abbreviations: ECT, ectoprocts; MED, mediuncus; BL, basal lobe.

APPENDIX 1. Recent county records of larval *Sialis* collected in Texas

COUNTY	STREAM	COLLECTION DATE	No. COLLECTED	COLLECTOR
Anderson	Box Creek	10 June 1999	11	D.E. Bowles
Bexar	Salado Creek	12 May 1998	4	D.E. Bowles
Bexar	Salado Creek	20 May 1998	3	D.E. Bowles
Bexar	Salado Creek	14 June 1999	1	D.E. Bowles
Brazos	Navasota River	14 July 1998	1	D E. Bowles
Cherokee	Box Creek	02 September 1998	2	D.E. Bowles
Colorado	Cummins Creek	20 July 1998	2	D E. Bowles
Comal	Comal Springs	07 September 2000	11	J.L. Locklin
Dallas	Tenmile Creek	01 June 1998	2	D E. Bowles
Dallas	Tenmile Creek	20 August 1998	2	D.E. Bowles
Gregg	Rabbit Creek	06 July 1998	2	D E. Bowles
Hays	San Marcos River	01 September 2000	2	J.L. Locklin
Lavaca	Lavaca River	11 June 1998	2	D E. Bowles
Leon	Buffalo Creek	03 August 1999	1	D.E. Bowles
Marion	Black Cypress Bayou	07 September 1998	1	D.E. Bowles
Menard	Ft McKavett Spring	February 1998	1	D.E. Bowles
Nacogdoches	Legg Creek	09 June 1998	3	D.E. Bowles
Panola	Mill Creek	09 September 1998	10	D.E. Bowles
San Jacinto	Winter's Bayou	15 June 1998	4	D.E. Bowles
San Jacinto	E Fk San Jacinto River	10 August 1998	2	D.E. Bowles
San Jacinto	E Fk San Jacinto River	04 October 1999	1	D.E. Bowles
Smith	Mud Creek	08 September 1998	6	D.E. Bowles

Appendix 2. North American Distributional Records of the six species of *Sialis* occurring in or near Texas.

The following North American distributional records are compiled from previous published records of Ross (1937), Whiting (1991), and Penny (1997) to give the most complete records of the six species found in Texas or in surrounding states. Additional new records are indicated by an asterisk (*) Records are arranged by Canadian Province (bold) with County or Internal Division, and the United States records are arranged by State (bold) followed by County. If no County follows State or Canadian Provinces, no specific county was indicated. Additional records were compiled using specimens from the Wilbur R. Enns Entomology Museum at the University of Missouri and the personal collection of Dr. David Bowles.

Sialis mohri Ross

CANADA: NB: York, **ON:** Essex, Kenora, Kent, Ottawa-Carleton **PQ.**
USA: AR: Montgomery, Pike, Washington. **CT:** New London, Tolland. **IL:** Champaign, Coles, Cook, DuPage, Edgar, Jackson, Kankakee, Lake, Marshall, Mason, Massac, McHenry, Montgomery, Morgan, Rock Island, Washington, Williamson, Winnebago. **IN:** Bartholemew*, Clark, Lake, Middlesex, Norfolk. **ME:** Aroostook. **MI:** Cheboygan, Crawford, Emmet, Iosco, Lenawee, Mackinac,Oscoda, Roscommon, Washtenah, Wayne, Wexford. **MN:** Anoka, Becker, Beltrami, Goodhue, Hennepin, Houston, Koochiching, Mille Lacs, Pine, Ramsey, Red Lake, St. Louis, Stearns, Todd, Washington, Winona. **MS:** Hinds, Lafayette, Rankin. **MO:** Boone*, Howard*, Macon*. **NE**. **NH** **NJ:** Morris, Ocean, Passaic, Rockland. **NY:** Oswego, Stockton, Westchester. **OH**. **OK:** Payne. **PA:** Luzerne, Monroe, Wayne. **RI:** Washington. **TN:** Lake, Obion, Shelby. **VT:** Caledonia. **WI:** Adams, Barron, Dane, Door, Milwaukee, Sauk, Vilas, Walworth, Winnebago.

Sialis infumata Newman

CANADA: ON: Ottawa-Carleton.
USA: AR: Garland, Pike, Washington. **IL:** Champaign, Cook, Jo Daviess, Kankakee, McHenry, McLean, Rock Island, Vermilion, Will. **IN:** Clark, Tippecanoe. **KS:** Pottawatomie, Riley, Wabaunsee. **KY:** Oldham, Rowan, Trimble. **MI:** Tuscola. **MN:** Lyon. **MO:** Boone*, Greene*, Macon*, Newton*,Pulaski*. **NC:** Wake **NJ:** Mercer. **NY:** Genessee, Onodaga, Tompkins. **OH:** Adams, Butler, Franklin **OK:** Pittsburgh. **PA:** Dauphin, Philadelphia, Snyder **SC**. **VA:** Fauquier, Rockingham. **WV:** Grant.

Sialis americana (Rambur)

USA: CT: New Haven. **DC:** Washington. **FL:** Alachua, Baker, Columbia, Highlands, Marion. **GA:** Wayne. **IN:** Lake. **LA:** East Baton Rouge, Iberville, St. James. **MD:** Prince, Georges. **MO:** Barton*, Johnson*. **MS:** Adams, Hinds, LaFayette. **NH:** Merrimack. **NJ:** Gloucester. **OH:** Summit. **SC**. **TX**. **VA:** Nansemond. **WI:** Grant.

Sialis joppa Ross

CANADA: ON: Thunder Bay.
USA: AR: Crawford, Fulton*, Montgomery. **CT:** New Haven. **DE. FL:** Liberty. **IL. KY:** Bullitt, Jeferson, Meade, Oldham **LA:** St. James **MD:** Montgomery **ME:** Cumberland. **MI:** Cheboygan, Newaygo. **MO*:** Phelps*, Pike*. **NC:** Buncombe, Jackson. **NH:** Coos. **NY:** Ontario, Schuyler, Tomkins, Ulster, Wyoming, Yates. **OH:** Jefferson, Noble. **OK:** Latimer. **PA:** Delaware, Montgomery, Philadelphia, Westmoreland. **VA:** Giles, Grayson, Page, Smyth. **VT:** Orleans. **WI:** Ozaukee **WV:** Pendelton, Summers

Sialis velata Ross

CANADA: AB BC MB ON: Bruce, Grenville, Hastings, Kenora, Ottawa-Carleton, Russell. **PQ:** Laprairie, Montreal. **SK**.
USA: CO: Larimer, Yuma. **CT:** New Haven. **DC:** Washington. **ID:** Bannock, Cassia, Fremont, Valley. **IL:** Champaign, Coles, Gallatin, Jersey, Johnson, Madison, Mason, Pope, Rock Island, Wabash, Washington, White. **KS:** Douglas, Franklin, Lyon*, McPherson, Pottawatomie, Riley. **KY**. **MA:** Middlesex, Norfolk. **MD:** Montgomery. **ME:** Lincoln, Penobscot **MI:** Arenac, Benzie, Cheboygan, Crawford, Gogebic, Ingham, Leelanau, Roscommon, St. Joseph, Washtenaw, Wayne. **MN:** Anoka, Becker, Beltrami, Cass, Clearwater, Crow Wing, Hubbard, Itasca, Lake, Mille Lacs, Morrison, Olmstead, Pine, Ramsey, St. Louis, Washington **MO:** Boone, Marion. **MT:** Flathead, Yellowstone. **NC**. **ND**. **NB**. **NH**. **NJ:** Rockland. **NY:** Albany, Clinton, Cortland, Hamilton, Onodaga, Ontario, Oswego, St. Lawrence, Tiogo, Tompkins, Yates. **OK:** Garfield. **TN:** Marion. **TX:** Bexar, Kerr, Travis, Williamson*. **UT:** Box Elder, Cache. **VA:** Appomattox, Giles, Montgomery, Page, Roanoke, Rockbridge, Shenandoah, Smyth, Wythe. **VT**. **WI:** Dane, Door, Vilas, Waukesha. **WV:** Jefferson. **WY:** Carbon, Crook, Laramie.

Sialis itasca Ross

CANADA: ON: Ottawa-Carleton **PQ:** Laprairie, St. Jean
USA: AR: Craighead **DC:** Washington **GA:** Bibb, Fulton. **IL:** Coles, Cook, Kankakee, Knox, Piatt, Winnebago. **IN:** Lagrange, Monroe, Noble. **KS:** Pottawatomie, Riley. **MD:** Montgomery. **MI:** Branch, Cheboygan, Monroe, Washtenaw. **MN:** Pine **MO:** Boone*. **NC:** Chatham, Wake. **ND:** Cass. **NY:** Chautauqua, Monroe, St. Lawrence, Tompkins **OH:** Huron, Washington **OK:** Marshall*, Payne **PA:** Dauphin. **TN:** Shelby **TX:** Brazos, Denton*, Limestone*, Travis*, Williamson* **VA:** Augusta, Fairfax, Greene, Rockingham. **WI:** Douglas. **WV:** Wayne.

APPENDIX 3. Physical and chemical characteristics of Town Lake and the San Gabriel River on 2 April 2001

	NO_3 (mg/l)	Ortho-P (µg/l)	Total P (µg/l)	Conductivity (meq/l)	TSS (mg/l)	Turbidity (NTU)
Town Lake	0.53	21 96	23.35	4.66	0.035	9.2
San Gabriel River	0.54	13.79	14.72	4.33	0.144	14.0