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DISTRIBUTION OF AQUATIC INSECTS ALONG A HYDROLOGIC
GRADIENT IN THE RUSSELL LAKES AREA,
SAN LUIS VALLEY, COLORADO

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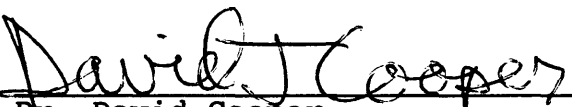
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A thesis submitted to the Faculty and the Board of Trustees of the Colorado School of Mines in partial fulfillment of the requirements of the degree of Master of Science (Environmental Science and Engineering).

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ABSTRACT

The study of aquatic insects in wetlands is essential for understanding how these areas function for production of waterfowl and non-game species of birds. A study was conducted of three wetland communities at Davey and Island Lakes in the Russell Lakes State Wildlife Area in the San Luis Valley of Colorado during 1991 to determine spatial and temporal abundance, biomass and species composition of aquatic insects. The aquatic, bulrush and sedge communities were studied at each lake. Water pH and conductivity were measured along with water standing depths and temperatures, lake surface water elevation changes, soil organic matter content and herbaceous standing crop. Aquatic insects were sampled monthly for six months. Detrended correspondence analysis (DCA) using species composition and abundance was used to determine species and sample stand distributions in the wetland communities. Environmental and vegetation variables were correlated to DCA stand scores to determine which variables may influence aquatic insect distributions.

The presence of aquatic vegetation strongly influenced insect distribution. The aquatic community plot at Davey Lake had low vegetation standing crop and had the lowest aquatic insect abundance and biomass. The adjacent bulrush community at Davey Lake had greater vegetation

standing crop with areas of detrital beds. The combination of the vegetation and detritus likely attributed to producing the highest aquatic insect abundance, biomass, and species richness in the bulrush community at Davey Lake. through the sampling season insect abundance and biomass generally declined at Davey Lake and increased at Island Lake.

Abundance, biomass, and species richness of the area were low compared to wetlands studied in other regions. The lack of aquatic vegetation in many of the lakes of this area limits production of aquatic insects and other invertebrates possibly affecting the number of waterfowl using the lakes as a feeding area.

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CHAPTER 1 INTRODUCTION

The importance of wetland communities in the production of aquatic macrophytes and aquatic invertebrates has been shown to be a major factor in the distribution, maintenance, and production of waterfowl. Aquatic insects and other invertebrates make up a sizable portion of the diet of many duck species (Swanson and Duebbert 1989). Aquatic insects accounted for 44 percent of the diet of female blue-winged teal during egg laying (Swanson and Meyer 1977). Young ducks are especially dependent on invertebrates as a food source (Ringelman 1991). Also, nongame species such as wading and shore birds are an important component of wetlands (Kroodsma 1979) and are likely to utilize invertebrates for food. Russell Lakes Wildlife Area (RLWLA) in the San Luis Valley of Colorado support a variety of bird species. The RLWLA also have many wetland community types. Wetland communities many times are segregated by depth of standing water (Stewart and Kantrund 1971). The distribution of aquatic insects in different wetland communities is essential to understanding production of avian species that utilize these communities for food acquisition.

This thesis examines aquatic insects in three wetland

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community types that occur along a hydrologic gradient determined by depth at two different lakes at the RLWLA.

The study objectives are:

- 1) Identification of the aquatic insect taxa present in selected wetland communities at RLWLA;
- 2) Calculation of temporal abundance and biomass distributions of aquatic insects in selected wetland communities;
- 3) Determination of the major factors controlling the distribution of aquatic insects in selected wetland communities;

This information is essential for determining relationships between wetland communities, environmental variables, and aquatic insects, facilitating the management of this area for avian production.

The physical position of aquatic insects in wetland communities is often determined by their morphological adaptations. Merritt and Cummins (1984) present a classification that describes the way aquatic insects maintain their position in wetland communities. These categories include skaters, planktonic, divers, swimmers, clingers, sprawlers, climbers, and burrowers. Another classification presented by Merritt and Cummins (1984) is based on "functional feeding groups" or feeding mechanism

that a particular aquatic insect exhibits. These include: shredders, collectors, scrapers, macrophyte piercers, predators, and parasites (Table 1). Both the physical location and functional feeding group are important in determining overall trophic status of aquatic insects (Lamberti and Moore 1984).

Spatial distributions of aquatic insects change with respect to: position in the water column, either benthic, planktonic or on some substrate; localized changes in micro-environmental conditions on a horizontal scale; and changes over wider areas due to environmental or substrate conditions (Minshall 1984). These factors contribute to the heterogeneity of the aquatic environment. Biotic and environmental factors add to this heterogeneity and are responsible for the contagious or patchy distribution of many aquatic insect communities (Elliott 1977).

Distribution of aquatic insects can vary by wetland community. Dvorak and Best (1982) studied macroinvertebrates on emergent and submerged vegetation in Lake Vechten, Netherlands, and found higher numbers and biomass of aquatic animals on an ash-free plant dry weight basis in the submerged zone than in emergent zones. However, when comparing plant densities emergent vegetation had a higher biomass of aquatic animals. Voights (1976), in a study of four prairie marshes in northwestern Iowa, found

Table 1. Functional groups represented by aquatic insects (after Merritt and Cummins 1984).

Functional Group

*** Shredders**

Dominant Food - Living and decomposing vascular tissue and coarse particulate organic matter (CPOM).

Feeding Mechanism - Herbivores and miners of live vascular tissue and detritivores and chewers of CPOM.

*** Collectors**

Dominant Food - Decomposing fine particulate organic matter (FPOM).

Feeding mechanism - Detritivores that filter organic matter suspended in the water column and collectors that gather fine particles that have settled on sediments.

Scrapers

Dominant Food - Periphyton - attached algae and associated material

Feeding Mechanism - Herbivores that graze by scraping mineral and organic surfaces.

*** Macrophyte piercers**

Dominant food - Living vascular plant tissue and cell fluids or filamentous algae cell fluids.

Feeding Mechanism - Pierce tissues or cells and suck fluids.

*** Predators**

Dominant Food - Living animal tissue.

Feeding Mechanism - Attack prey and ingest whole animal or pierce cells and tissue and suck fluids.

Parasites

Dominant Food - Living animal tissue

Feeding Mechanism - Internal parasites of eggs, larvae, and pupae. External parasites of larvae, prepupae and pupae in cocoons, pupal cases or mines.

* Functional feeding group collected at Davey and Island Lakes, Russell Lakes Wildlife Area, Saguache County, Colorado, 1991.

numbers of chironomids and caenid mayflies to be greater in the submergent vegetation and Odonata nymphs fairly equally distributed between the emergent and submerged communities. Submerged vegetation protected from wind by emergent vegetation produced greater numbers of chironomid larvae (Voights 1976).

The amount of plant biomass may also have an effect on the distribution of aquatic insects. Krull (1970), in a study of Cayuga Lake in central New York, found that invertebrate abundance increased with an increase in plant biomass. Abundance reached its peak soon after the plants appeared and sixty percent of the invertebrates were found on three or fewer plant species.

Within communities, distributions of aquatic insects may also vary. Studies conducted by Krecker (1939) in the western part of Lake Erie, found characteristics of submerged vegetation, primarily the degree of leaf dissection, influenced distribution of aquatic macroinvertebrates. Krecker's study factored out many environmental variables that influence insect distributions by choosing a study site with plant species of different morphology growing closely together. Conversely, Cyr and Downing (1988) studied ten lakes around Montreal, Quebec, finding the number of epiphytic invertebrates per unit plant biomass generally showed no relationship to leaf dissection,

except for Myriophyllum, which harbored more invertebrates. Rosine (1955) studied three aquatic macrophyte genera, Chara, Polygonum, and Potamogeton, each exhibiting different degrees of leaf dissection, in Muskee Lake, Colorado. Findings were that the more dissected plant Chara supported higher densities of organisms but also grew in denser beds than the other two genera. A study by Chilton (1990) at Lake Onalaska, Wisconsin, found the damselfly Enallagma sp. was almost exclusively associated with Ceratophyllum, and other invertebrates utilized plant surfaces differently over the season. Plant factors besides morphology that may determine epiphytic invertebrate abundance include surface texture, epiphytic algae growth and nutritional differences, nutrient content of plant tissues, and presence of defensive chemicals (Cyr and Downing 1988).

Abiotic components such as detritus and mineral substrates can influence aquatic insect distributions. Generally, aquatic macrophytes support higher densities of aquatic invertebrates than do mineral substrates, larger inorganic particles support greater numbers than fine particles, and aquatic insects show preference for a particular substrate size and type (Minshall 1984). Tebo (1955) found that densities of bottom fauna were greater in sand and gravel bottoms compared to numbers in clay and silt bottoms. Fine textured mineral substrates may produce

turbid conditions under certain circumstances. Both quantity and quality of light are affected by dissolved materials and suspended solids, influencing the maximum depth plants can root and survive (Riemer 1984) in turn affecting aquatic insect distributions.

Organic matter can attract aquatic insects by acting as a food source. Studies by Vodopich and Cowell (1984) found the chironomid larvae Procladius culiciformes (Linnaeus), a predator, was attracted to higher levels of organic matter, possibly due to a greater availability of prey or for use as an alternate food source. However, highly organic sediment showed a negative correlation to P. culiciformes numbers possibly due to decreased oxygen concentrations.

Many factors influence distributions of aquatic insects. The results of the cited studies sometimes are contradictory and no consistent model can be applied in describing these distributions.

CHAPTER 2 STUDY AREA

2.1 General Description

The RLWLA is located in the northwestern side of the San Luis Valley, 14 kilometers south of the town of Saguache, Saguache County, in south-central Colorado. The elevation of RLWLA is approximately 2300 meters above sea level. Annual precipitation at Saguache averages 21.7 cm with total precipitation for the 1991 sampling year being 20.9 cm (National Climatic Data Center 1991). Saguache's average annual air temperature is 5°C and the growing season is about 119 days. Mean winter temperatures are -5.6°C and mean summer temperatures are 16.7°C (USDA 1984). Winds can be strong and sustained, particularly in the spring.

The San Luis Valley is a large intermountain basin that topographically has a flat floor except for high dune ridges that occur on the east side of major lakes. Surface soils in the RLWLA area range from fine sand to clay loams and are generally alkaline in nature (USDA 1984). Dominant upland flora of the valley in this area is dominated by Sarcobatus vermiculatus (greasewood) and Distichlis stricta (saltgrass).

2.2 Russell Lakes Wildlife Area

Four major lakes occur at RLWLA (Fig. 1). The lakes, Davey, Trites, Harrence, and Island generally are shallow and managed to hold water through the year with the aid of headgates. Artesian wells and a regionally high water table contribute to maintain lakes water levels and provide support for wetlands in the area. The two lakes in which this study took place are Davey and Island Lakes. Davey Lake, topographically, is the highest lake and Island Lake the lowest in the RLWLA, with an elevation difference of 0.6 meters over a distance of 1.3 km. Northwest of Davey Lake, a freshwater artesian well flows approximately 0.09 m³/sec. and is a major source of water input. Water supplied to Island Lake enters on the west side flowing from Davey through Harrence Lake and from Trites Lake.

2.3 Wetland Communities at RLWLA

Several different wetland types are found in the RLWLA, varying from those in permanent standing water to those having seasonal or permanent high water tables but without permanent standing water. The western lakes, Trites and Davey, have permanent standing water and their western borders contain large areas of emergent vegetation (hardstem bulrush). Aquatic vegetation is sparse in these two lakes and is uncommon adjacent to the hardstem bulrush. Sedges

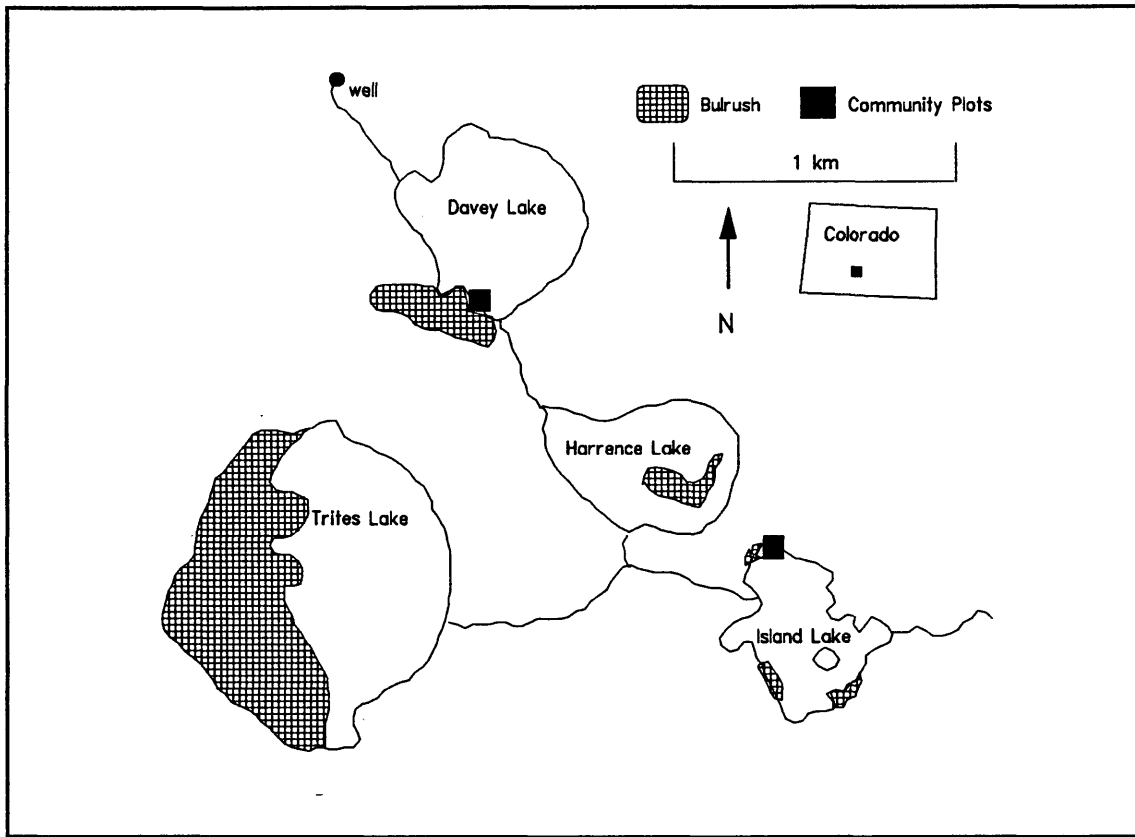


Figure 1. Map of Russell Lakes Wildlife Area, Saguache County, Colorado, showing locations of community plots.

are frequent outside the bulrush and in some areas arctic rush is common. The eastern side of these two lakes are bordered by high dune ridges. Vegetation in the littoral zone on the eastern side is sparse due to wind and wave action. Harrence and Island Lakes differ from Davey and Trites Lakes. They are shallower, do not have extensive areas of hardstem bulrush on their western borders, lack dune ridges on their eastern margins, and sedges, baltic rush and three square are common around the edges. Little submerged vegetation is present at Harrence Lake where Island Lake supports fairly dense stands.

Small basins with high water tables but without permanent standing water are numerous at RLWLA. These areas have standing water through parts of the summer, usually after a significant rainstorm. Salts concentrate at the soil surface and accumulate in these basins due to runoff creating relatively high water conductivities. Vegetation in these ephemeral wetlands can be lacking or be dominated by annual plant species.

2.4 Wildlife of the RLWLA

Many waterfowl and nongame species of birds occur at the RLWLA. Waterfowl include mallards, cinnamon teal, green winged teal, Canada geese, ruddy ducks, red heads, and coots. The San Luis Valley is considered one of the most

important duck breeding areas in Colorado (Colorado Division of Wildlife 1989). Nongame species observed were American avocet, black-crowned night heron, western grebe, marsh wren, Wilson's phalarope, white-faced Ibis and snowy egret. A few muskrats were observed in Island Lake. Carp were present in the lakes and in some of the smaller water ways. Several species of smaller fish were observed in ephemeral small ponds adjacent to Island Lake.

CHAPTER 3 METHODS

3.1 Study Design

Three wetland communities were selected at each of two lakes for the collection of aquatic insect samples and environmental and vegetation data. Three communities were selected to represent a hydrologic gradient that changes by standing water depth. From deepest to shallowest the communities are 1) aquatic, 2) bulrush and 3) sedge. Community plots were established at each lake. Sampling of vegetation and detritus for aquatic insects was conducted at monthly intervals to determine biomass, abundance, and species richness. Temperature and water depths for each stand were collected at this time. Water chemistry measurements for pH and conductivity were collected three times. Soil samples were collected for determining soil organic matter content. Vegetation was sampled once for standing crop.

Detrended correspondence analysis (DCA) was performed with the computer software package CANOCO (Ter Braak 1984) to compare aquatic insect composition and abundance for all community plots. Environmental variables were correlated to CANOCO sample scores using Spearman rank correlation. Two sample t-tests were performed on abundance and biomass data,

both between similar communities at the two lakes and between the aquatic and bulrush communities at each lake.

3.2 Selection of Wetland Communities, Plots, and Stands

A stratified random sampling design (Green 1979) was used to sample the three wetland communities at RLWLA.

Plots were established to represent:

- 1) the aquatic community, composed of Hippuris vulgaris, Potamogeton pusillus and Zanichellia palustris were submergent species rooted to the substrate.
- 2) the bulrush community, composed of Schoenoplectus lacustris subsp. acutus which were rooted plants having their basal portions in shallow water and had leaves and stems present primarily in the air.
- 3) the sedge community, composed of Carex lanuginosa and C. nebraskensis which grow in areas that were infrequently flooded throughout the season.

(Plant nomenclature follows Weber 1990)

These communities were selected because they characterize much of the wetland habitat associated with the lakes at RLWLA.

Individual community plots along the hydrologic gradient were selected to be adjacent to each other. For the sedge community at Davey Lake an area approximately 30 m

away was chosen because the area represented by the sedge adjacent to the bulrush community was too small to obtain sufficient samples through the season. Plots were different in size corresponding to natural boundaries of the community. A wooden lath was used to mark the corners of each plot. Plot borders were well within the communities to eliminate "boundary effects" of the ecotones (Chambers and Brown 1983).

Sample stands for each community were selected by use of a random number table. Two adjacent plot sides were selected and random numbers were picked to represent distance, in feet, along each of these sides (Kieth 1988). One corner was chosen as the starting point and the two distances were paced off to determine the location of the sample stands. Sample stands were marked with a pin flag in the northwest corner so that the likelihood of sampling the same spot would be eliminated. Each month, three stands were sampled for each plot at each lake. If no part of the community had standing water, the community was not sampled. If the community was only covered partially with standing water, only those areas with standing water were sampled.

Nomenclature used in this thesis is as follows:

- Community plots was the area representing each of the three communities at each of the two lakes in which sample stands were located. Six community plots were established

in this study.

- Sample stands were the actual location from which aquatic insects, detritus, vegetation, water depth and temperature measurements were collected.

- Samples were the aquatic insects collected from the sample stand.

3.3 Environmental and Vegetation Measurements

Lake surface water elevations were measured over the sampling season (Cooper and Severn 1992). Permanent staff gauges were installed at each lake and water levels were recorded weekly. Water depth was measured at each sample stand from the center of the sampler with a retractable tape measure.

Bottom temperatures for each stand were obtained using a Taylor model 5622 swimming pool thermometer. The thermometer remained on the bottom while the sample was being collected to give sufficient time for temperature stabilization.

During insect sorting, qualitative data was kept on the amount of different size fractions of coarse detritus (>1 mm) in each sample. Coarse detritus remaining after sorting was placed into a container with water and the detritus thickness was measured.

Determination of soil organic matter was conducted once

in October. A composite sample from two cores (core size 6.7 cm in diameter by 10.0 cm deep) were randomly collected from each of the aquatic and bulrush community plots to a depth of 10 cm. Samples were oven dried at 105°C for 24 hours, weighed, placed in a muffle furnace for 24 hours at 550°C to oxidize the organic matter, then reweighed (Standard Methods 1989). Soils were weighed to the nearest 0.01 grams.

Measured environmental variables for water were hydrogen ion activity (pH), conductivity, and dissolved oxygen. Many of these measurements were not taken coincident with aquatic insect sampling. pH measurements were measured three times over the season, at mid-day each time, using an Orion model 250 A pH meter. Calibration was conducted several times daily using pH 7 and 10 buffer solution. Conductivity was measured three times over the season with an Orion model 122 conductivity meter. Dissolved oxygen measurements were obtained once in September using a Yellow Springs Instrument model 54 A oxygen meter. Calibration of the dissolved oxygen meter was done using air saturated water and surface elevation.

Plant communities were sampled to determine standing crop (Cooper and Severn 1992). A 0.2 m² quadrat was randomly placed in the community and all live vegetation rooted within was clipped and placed in paper bags (Chambers

and Brown 1983). Samples were air dried and weighed and are reported as grams/m². Counting of live bulrush stems was done during insect sorting to determine stem density.

3.4 Insect Collection and Analysis

A modified design of a Model A Gerking sampler (Gerking 1957) was constructed for the quantitative collection of aquatic insects, associated vegetation, and detritus. The base frame was constructed of 2.5 mm thick plate steel. The inside dimension of the base frame was 30.48 cm (one foot) on each side and had a height of 9 cm. Attached to, and extending above the base frame for 15 cm, is a porous fabric with a mesh size of less than 0.5 mm (range approximately 0.2-0.3 mm). Beyond this extending upward was a canvas sleeve 56 cm long, giving an overall sampler height of 81 cm. The diameter of the opening at the top was approximately 40 cm. At the top of the canvas, a ring of flexible foam water pipe insulation was secured to prevent the canvas from sinking much below the surface of the water and allowing insects to escape. At the base of the steel frame, on one side, was a horizontal slot into which a steel bottom plate was inserted, traveling along a rail sealed on the upper edges by flexible weather stripping. A slip-in handle and foot pegs were added for stabilization while the sampler was being forced into the bottom sediments.

Sampling of all six community plots was completed over a 10 hour period. Sampling dates were on 29 May, 15 June, 19 July, 23 August, 18 September, and 21 October, 1991. The sampler was placed over the vegetation, using the pin flag as a placement guide for the northwest corner, and forced into the sediment which sealed the sampler preventing the escape of aquatic insects. When sampling the bulrush community, vegetation above the surface of the water was clipped with pruning shears before placement of the sampler. Clipped vegetation was discarded outside the community plots. It is possible that during clipping many of the more mobile aquatic insects swam from the sample area. Vegetation was cut at the sediment/detritus surface. To collect the detritus, bottom material inside the sampler were suspended by hand agitation of the water, then the bottom door was quickly closed and locked. In aquatic communities, an estimated 4 cm of top sediment and detritus was collected by the sampler, where as in bulrush communities the amount was variable depending on substrate thickness and the amount of matted root material present. The sampler was then taken to shore, drained of most of the water through the fabric and the contents of the sampler placed into a large marked plastic bag. Samples were placed immediately into a cooler which contained ice and held there until they were sorted over the next 48 hours.

Sampling of the sedge plots was done with a quadrat due to lack of standing water. The quadrat was 30.48 cm (one foot) on each side. Stands which were saturated to the surface or had standing water were sampled. Vegetation was clipped approximately 3 cm above the ground surface and discarded outside the plot. The remaining vegetation and detritus to a depth of approximately 1 cm was collected by hand and placed in a plastic bag. Samples were then placed in a cooler with ice.

Sorting consisted of washing the sample material through a U.S.A. standard sieve no. 35, 0.5 mm opening (Reish 1959), discarding that portion which passed through. Placing a small amount of detritus and/or plant material into a white porcelain lined pan, insects were removed by hand. Insect samples were preserved in a 5 percent (Kondratieff et al. 1990) unbuffered formalin solution. Samples were further sorted to taxonomic groups and identified, with the aid of a dissecting microscope, to genus when possible using Merritt and Cummins (1984). A record of total numbers per taxon was kept. Samples were identified further to species when possible. The midge family, Chironomidae, and many of the beetles, Coleoptera, were not identified to species.

Insect samples were oven dried at 103 °C for 24 hours and dry weights were recorded by species to the nearest

0.0001 grams (Mason et al. 1983). Members of the Chironomini tribe were treated as a group for biomass measurements despite that Cryptochironomus sp. is considered a predator (Merritt and Cummins 1984) whereas Chironomus sp. and Dicrotendipes sp. are representatives of the collector functional group. Likewise the subfamily Tanypodinae were treated as a group for biomass measurements and were represented by the genera Larsia and Procladius, both of which are predators. Hesperocorixa laevigata and Sigara alternata in the family Corixidae were treated in a similar manner as both are macrophyte piercers. Dry weights used for calculations were not adjusted for weight loss from the effects of formalin preservation. Since all the samples were dried at the same time, some specimens were in formalin for up to 250 days. Leuven et al. (1985) found that different taxa responded differently to the same concentration of preservatives stored over the same amount of time. Different preservation times and the number of different taxa studied would have made standardization of dry weights difficult to compute accurately.

3.5 Classification of Aquatic Insects

Classification of aquatic insects was done both for species taxonomy and for functional feeding groups. Ecologically, the use of functional groups provides

information concerning sources of food and nutrition which are available in wetland communities for aquatic insects and provides information on the role aquatic insects play in the community. Functional groups are approximations of the feeding habits of aquatic insects as many are generalists with variations seen through age and also within the same species in different habitats (Cummins 1973).

Classification of the collector functional group includes both collector gatherers and collector filterers. In this study, community function was examined indirectly by classifying aquatic insects into functional groups based on their mode of feeding (Table 1; Merritt and Cummins 1984).

3.6 Statistical Analysis

Detrended correspondence analysis (DCA) was performed using the computer program CANOCO (Ter Braak 1988). DCA is useful in many ecological studies for comparing species composition from a series of samples. Points closer together have species composition more similar than points that are farther apart (Jongman et al. 1987). DCA can be used to analyze species occurrence patterns and helps connect species and community relationships to specific environmental variables. Following ordination, interpretation of ordination axis stand scores to environmental variables was conducted using Spearman rank

correlation analysis to determine which variables may influences distribution along each of the four axes. Two sample t-tests were performed to compare abundance and biomass measurements in the lakes and communities. The sedge communities were not compared due to small sample size as they were not sampled on all months. A normal distribution was assumed.

CHAPTER 4 RESULTS AND DISCUSSION

4.1 Environmental and Vegetation Measurements

Elevation of surface water in each lake varied over the sampling season. Figure 2 displays the relative changes in surface water elevation for the two lakes. Both lakes displayed the same general fluctuation timing, with Davey Lake having greater amplitude until mid July. Island Lake reached its lowest elevation on 24 July. In September Davey Lake rose to its highest levels whereas Island Lake dropped from its season high in August to near average lake levels. Maximum fluctuation was about 17 cm at Davey Lake and 7 cm at Island Lake. Peaks in surface water elevation flooded outer regions of the bulrush community at Davey Lake and flooded or saturated portions of the sedge community at both lakes, increasing the habitat for aquatic insects. At Island Lake, due to the flatter topography around the lake, larger areas of sedge were in standing water as were other wetland communities not sampled, i.e. Juncus articus (arctic rush) and Schoenoplectus pungens (three square), improving the opportunity for other aquatic insects to migrate into the sedge community.

Standing water depth at the stands were greater in the aquatic plots with a mean depth of 56.4 cm (range 45.7-70.1

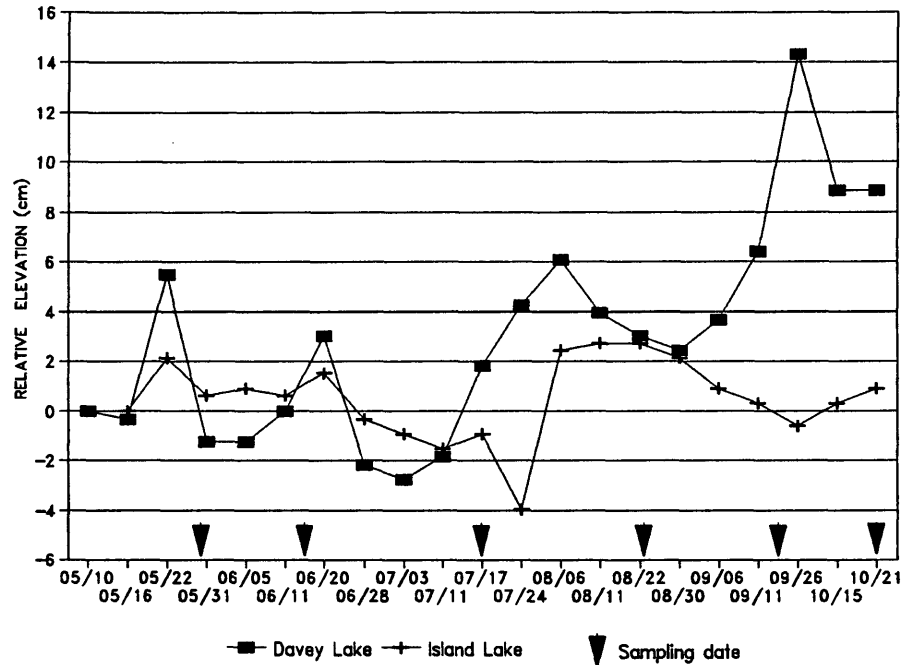


Figure 2. Relative surface water elevation of Davey and Island Lakes at the Russell Lakes State Wildlife Area, Saguache County, Colorado, 10 May - 21 October, 1991.

cm) and 36.0 cm (range 25.0-39.6 cm) for Davey and Island Lakes respectively. Nearly a 20 cm difference in mean standing water depth existed between these two plots. Bulrush plots were similar between lakes with seasonal means of 26.0 cm (range 3.7-47.2 cm) at Davey Lake and 22.2 cm (range 12.8-30.4 cm) for Island Lake. Mean water depth at the sedge community plot at Davey Lake was 1 cm (range 0.6-

4.2 cm) where at Island Lake, stands were only saturated to the surface and water depth was not be measured.

Mean water depth of the sample stands show the hydrologic gradient for the community plots. Davey Lake displayed the greatest water depth gradient difference from the sedge to the aquatic plot and Island the least. Island Lake appeared to be more stable with respect to the hydrologic regime of wetland communities due to less change in surface water elevation and in the sampling depths within each plot.

Water temperatures recorded in May were near or at their highest for plots at Island Lake (Fig. 3). Maximum temperatures for plots at Davey Lake peaked in July. In June the aquatic plot at Davey Lake was 4°C or more cooler than the other plots. Water temperatures are affected by the water depth of the stand so shallower depths should show higher temperatures. Temperatures between plots had the greatest range on 15 June of nearly 5.5°C. A decline in temperatures at Davey Lake started between 17 July and 23 August whereas Island Lake declined later from 23 August to 18 September. A steady decline in temperature for all plots was seen between 18 September and 21 October. Through July and later in October temperatures between plots at Island Lake showed less difference than those at Davey Lake. Island Lake appeared to be more stable with respect to

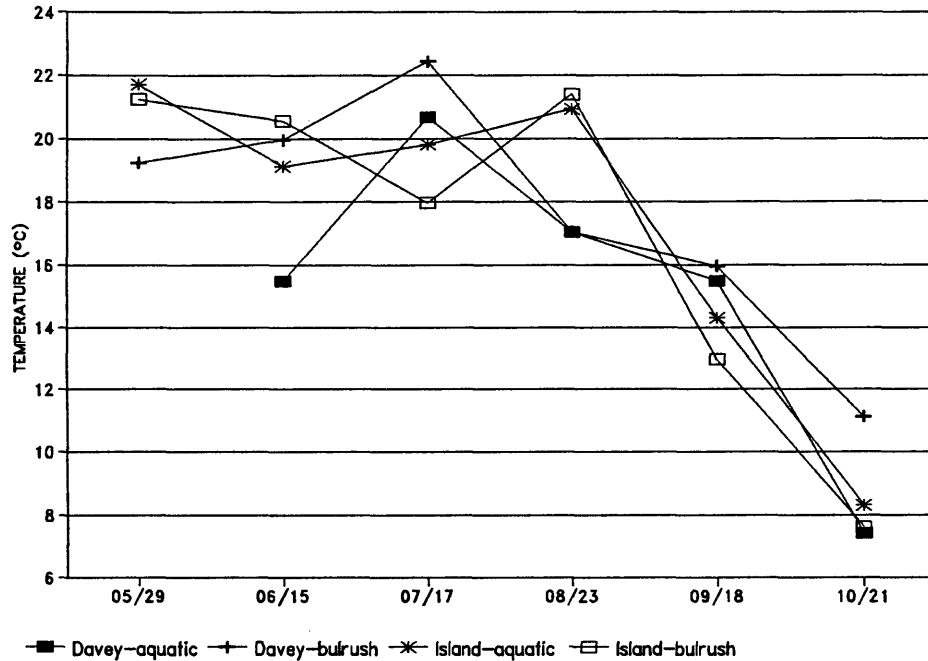


Figure 3. Water temperature ($^{\circ}\text{C}$) at sampling depth for stands at Davey and Island Lakes, Russell Lakes Wildlife Area, Saguache County, Colorado, 5 May - 21 October, 1991.

changes over the season in temperature.

Both the aquatic and bulrush communities at each lake were sampled for organic matter content. Organic matter content at the aquatic plot at Davey Lake had 13 percent by weight. The aquatic plot at Island Lake had an organic matter content of 9 percent. The bulrush plots had less organic matter in the soil. Davey Lake had an organic

matter content of 7 percent and Island Lake had a content of 5 percent.

Soil organic matter was highest in communities at Davey Lake due likely to accumulation of plant material produced by large areas of bulrush adjacent to the community plots. Field and laboratory notes indicate that some bulrush community plot sample stands at Davey Lake had larger volumes of coarse particulate organic matter (>1.0 mm), primarily consisting of partially decomposed bulrush stems. Surface currents induced by wind play a role in distribution of material (Barton 1980) and much of the material here likely originated from the large bulrush areas to the west of the plots. Murkin (1983) found that the comparative rate of decomposition for bulrush was rapid with only 20 percent of the dry weight remaining after one year. At this rate, accumulation of bulrush detritus would be possible.

Organic matter has variable effects on the distribution of aquatic insects. Some insects use organic matter as a food source where some Trichoptera may use it for case building (Minshall 1977). As to be shown in a later section, no Trichoptera were collected at Island Lake and the mayfly Caenis punctata seemed to prefer Davey Lake and apparently was associated with the thicker detrital layers. It is suspected that the organic matter content and type had an influence on the distribution of these insects, and

possibly others.

Water conductivity for the lakes is presented in Table 2. On all dates, conductivity between lakes was lower at Davey Lake. The maximum conductivity for Davey Lake occurred in mid-June. In October, Davey Lake dropped to its lowest conductivity where as Island Lake remained near its highest level. Conductivity increases latter in the season at Island Lake could be related to evaporation from the lake concentrating the salts. Overall, changes in conductivity were small.

Water conductivity at the lakes was low for the range natural waters exhibit (Hem 1959). A study by Euliss *et al.* (1991) of drainwater ponds in California found the water boatman Trichocorixa reticulata Guerin and the midge Tanytus grodhausi Sublette were commonly found in waters with conductivities ranging from 10 to >70 mmhos/cm with only T. reticulata found in ponds with conductivities of 300 mmhos/cm. These extremely high conductivities were determined to be the cause for low biotic diversity in these ponds. Moore (1980) also found that conductivities around 2000-3000 μ mmhos/cm may inhibit development of certain taxa. Conductivities at the two lakes were well below those in the cited studies and probably would not have had an influence on the majority of aquatic insects present.

Hydrogen ion concentration (pH) was similar between

Table 2. Water conductivity ($\mu\text{mhos/cm}$) and pH for Davey and Island Lakes, Russell Lakes Wildlife Area, Saguache County, Colorado, 1991.

Location	19 June		13 August		15 October	
	cond.	pH	cond.	pH	cond.	pH
Davey outlet	271	8.78	239	9.15	202	9.51
Island outlet	295	8.84	350	9.22	348	9.48

lakes through the season, never more than 0.07 pH units different on the same dates, and increased in both lakes over the season (Table 2). A study by Driver (1977), conducted in small prairie ponds in central Saskatchewan, found that 61 percent of chironomid species were found between a pH range of 6.0 to 9.2 and 33 percent in water more alkaline. The pH ranges for Davey and Island Lakes fell in the range of these two categories and it is likely that some influence was exerted by pH on species richness. Additionally, a study by Wrubleski (1984) in the Delta Marsh, Manitoba, Canada, accounted for 84 species of Chironomidae, which he determined was not a large number of species compared to other intensively studied lentic habitats. In this study only 7 chironomid taxa were identified, a comparatively low number possibly caused by pH or other factors.

Dissolved oxygen was measured in the aquatic and bulrush communities during September. Vegetation was still green but probably not growing at its peak. At Davey Lake, the aquatic community plot had higher dissolved oxygen levels early in the day and the bulrush community later (Figure 4). At Island Lake the aquatic plot had higher oxygen levels early and both communities were nearly the same later in the day. The oxygen levels at Davey Lake were generally higher than Island Lake for both community plots. Temperatures at 05:30 hours for plots at Davey Lake were both 13°C and for Island Lake 13.5 and 14.0 °C for the aquatic and bulrush plots respectively. Temperatures at 14:00 hours for Davey Lake were 17.5 and 18.5°C for the aquatic and bulrush plots respectively, and were 20.5°C for the aquatic plot and 21.0°C for the bulrush plot at Island Lake. The higher dissolved oxygen levels at Davey Lake could be accounted for in several ways. First, the water temperatures at Island Lake were warmer through the day and would hold less oxygen. Secondly, Davey Lake was exposed to more wind action and diffusion of oxygen into the water would be enhanced. The steep rise later in the day at Island Lake is probably attributed to the production of oxygen by plants. Both plots at Island Lake showed a decrease in dissolved oxygen after sunrise and could be attributed to aquatic invertebrate, microbial and plant

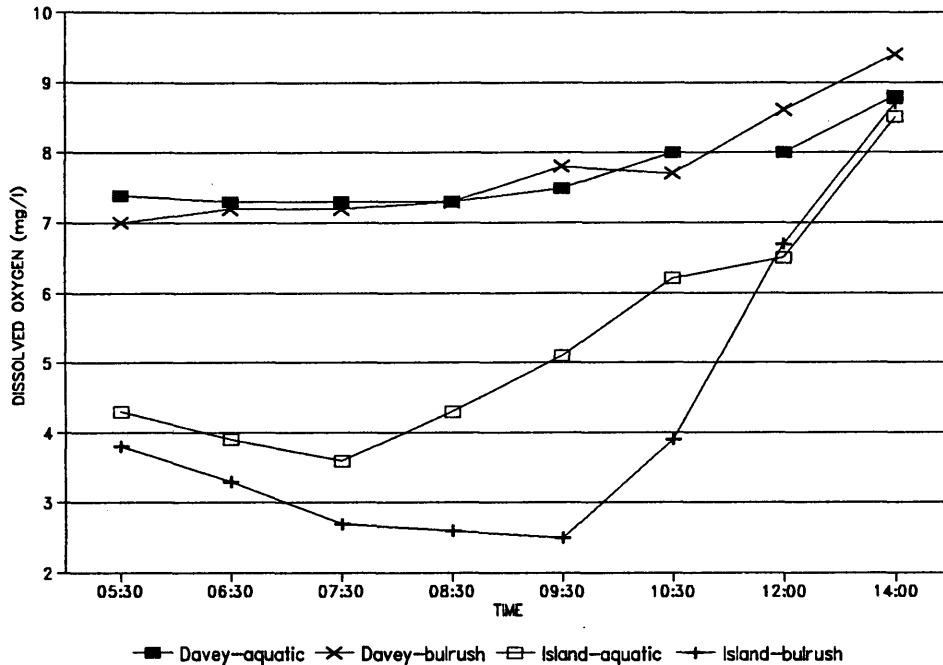


Figure 4. Dissolved oxygen (mg/l) in the aquatic and bulrush plots at Davey and Island Lakes, Saguache County, Colorado, 11 September 1991.

respiration.

Minimum oxygen levels for survival vary by species and generally, lentic organisms tolerate lower levels than lotic organisms (Minshall 1984). Gaufin *et al.* (1974) found that mayflies had a low tolerance to reduced oxygen levels followed by caddisflies, true flies, and damselflies, in that order. Minimum levels for species collected in Utah

were 3.3 mg/l (29 percent saturation) for mayflies with average survival of 10 days down to 2.2 mg/l (19 percent saturation) for damselflies with an average survival of 39 days. Oxygen levels approached these lower levels in the bulrush plot at Island Lake but only for a period of around four hours. Oxygen stress appeared to be less at Davey Lake and, as to be seen later in the data, more mayflies were at this lake.

Vegetation in the aquatic plots at Island Lake was dominated by Hippuris vulgaris (mares-tail), Potamogeton pusillus (pondweed) and Zanichellia palustris (horned pondweed) (plant species nomenclature follows Weber 1990). The vegetation in this plot remained green through the sampling season and experienced little die back. The aquatic community plot at Davey Lake was nearly devoid of aquatic vegetation with only a small representation of P. pusillus. Dominant vegetation of the bulrush community plots was similar at both lakes, having primarily Schoenoplectus lacustris subsp. acutus (hardstem bulrush) with lesser amounts of Myriophyllum spicatum (water-milfoil) and Utricularia ochroleuca. The sedge community of both lakes was dominated by Carex nebraskensis and C. lanuginosa (Cooper and Severn 1992).

Vegetation biomass at Island Lake produced more than ten times the herbaceous standing crop of bulrush as did the

bulrush plot at Davey Lake (Table 3; Cooper and Severn 1992). Live bulrush stem densities were nearly three times greater at Island Lake than Davey Lake in the bulrush plot. No herbaceous data was taken for the aquatic community at Davey Lake, however insect sampling produced very little plant biomass in the sampler, and when present was usually Potamogeton pusillus. In the sedge plots, only Island Lake was sampled for herbaceous standing crop but the standing crop for the sedge plot was probably similar at Davey Lake.

Herbaceous standing crop was greater at Island Lake. The aquatic plot at Davey Lake produced little vegetation. Aquatic vegetation serves as a substrate on which aquatic insects both dwell and obtain food. Insects such as Ischnura are classified as climbers and prefer vegetation. Climbers were nearly absent in the aquatic plot at Davey Lake (Table 4). High stem density of bulrush may have had an effect on species richness. The bulrush plot at Davey Lake supported 23 taxa where as the more dense bulrush stands at Island Lake only supported 15 taxa. Some mayflies, caddisflies, and chironomid have shown preferences to different degrees of shading (Minshall 1984). In this study the caddisfly Hydroptila ajax was found only at Davey Lake in the less dense bulrush. This may be attributed to the greater degree of shading at Island Lake effecting light intensity and water temperatures. Other factors such as

Table 3. Herbaceous standing crop (data from Cooper and Severn 1992) and live bulrush stem density of plots at Russell Lake Wildlife Area, Saguache County, Colorado, 1991.

Plot	Standing Crop (g/m ²)	Live Bulrush (number of stems/m ²)

Davey Lake		
Bulrush	173.5	77.5
Sedge	339.5	
Island Lake		
Aquatic	205.0	
Bulrush	1780.5	213.1

relative wave action, which may affect oxygen saturation, and the amount of suspended sediment in the water may also explain this distribution.

4.2 Aquatic Insect Distributions

Aquatic insects distributions are presented comparing the two lakes, the three communities at each lake and changes over the sampling season. Abundance and biomass are presented along with individual weights.

4.2.1 Aquatic Insects of the Study Area

A total of 34 aquatic insect taxa representing 6 orders were identified in the RLWLA study area during the 1991 sampling season (Table 4). A complete species list with

common names is in Appendix A. Many species were found at only one lake or community plot and often were represented by single specimens. The Chironomidae (midge), Hemiptera (true bugs), and Ephemeroptera (mayflies) were collected at each lake and from most community plots. Members of the order Trichoptera (caddisflies) were collected only at Davey Lake. Odonata (damselfly and dragonflies) were present only in the bulrush plot at Davey Lake, but were present in all three community plots at Island Lake. Coleoptera (beetles) were present in both lakes, but different taxa occurred between lakes. At Davey Lake the bulrush plot had the greatest number of taxa for all communities sampled with 23, and the sedge plot the least with 6 taxa. The aquatic and bulrush plots at Island Lake had similar numbers of taxa.

From this data it is clear that between community differences in species richness can occur. A community at one lake may favor a specific group of taxa that may be lacking in the same community at the other lake. Examples of this is the bulrush community plot at Davey Lake having Trichoptera where Island Lake had none and in the differences of the Coleoptera taxa between lakes. Some aquatic insects like the Chironomidae were found in all communities. Environmental variables were likely to play a role in determining where these insects occur and are discussed later in the thesis.

Table 4. Aquatic insect taxa functional group, habit, and distribution with total number of species in each community at Davey and Island Lakes, Russell Lakes Wildlife Area, Saguache County, Colorado, 1991. For functional groups C = collector, P = predator, PI = piercer-herbivore, S = shredder. For habit B = burrower, PL = planktonic, SP = sprawler, C = clingers, CL = climbers, SW = swimmers, SUR = surface, D = divers.

Order Family Genus	Functional Group	Habit	Davey Lake			Island Lake		
			aquatic	bulrush	sedge	aquatic	bulrush	sedge
Diptera								
Tipulidae	S	B			++			
Culicidae								
Anopheles sp.	C	PL						++
Ceratopogonidae								
Culicoides	P	B		++				
Chironomidae								
Tanypodinae*	P	SP	++	++		++	++	++
Cricotopus sp.	S	C		++		++		
Chironomus sp.	C	B	++	++		++	++	
Cryptochironomus sp.	P	SP	++			++	++	
Dicrotendipes sp.	C	B	++	++	++	++	++	++
Tanytarsus sp.	C	CL&C	++	++	++	++	++	++
Dixidae								
Dixa sp.	C	SW					++	++
Tabanidae								
Chrysops sp.	P	SP		++				
Dolichopodidae	P	SP			++		++	
Ephydriidae	C	B		++		++	++	++
Scathophagidae	S	B			++			
Hemiptera								
Corixidae								
Hesperocorixa laevigata**PI		SW&CL	++	++		++	++	++
Trichocorixa calva	P	SW&CL	++	++		++		
Ephemeroptera								
Baetidae								
Callibaetis ferruginea	C	SW&CL	++	++		++	++	++
Caenidae								
Caenis punctata	C	SP	++	++		++	++	
Coleoptera								
Gyrinidae								
Gyrinus sp.	P	SUR						++
Halapidae								
Halipus sp.	PI	CL					++	
Dytiscidae								
Celina sp.	P	SW&CL					++	++
Hydroporus sp.	P	SW&CL		++				
Rhantus gutticollis	P	SW&D		++				
Hydrophilidae								
Berosus sp.	PI	SW&D		++	++			
Staphlinidae	P	C&CL						++
Curculionidae	S	C&SP		++				

* Subfamily includes Larsia sp. and Procladius sp.

** Includes some Sigara sp.

(continued)

Table 4. (continued)

Order Family Genus	Functional Group	Habit	Davey Lake			Island Lake		
			aquatic	bulrush	sedge	aquatic	bulrush	sedge
Odonata								
Aeshnidae								
<u>Anax junius</u>	P	CL		++		++	++	
Coenagrionidae								
<u>Ischnura perparva</u>	P	CL		++		++	++	++
Trichoptera								
Hydroptilidae								
<u>Hydroptila ajax</u>	PI	CL		++				
Phryganeidae								
<u>Phryganea</u> sp.	S	CL		++				
Leptoceridae								
<u>Mystacides</u> sp.	C	SP&CL		++				
<u>Oecetis</u> sp.	P	C&SP		++				
<u>Triaenoides</u> sp.	S	SW&CL		++				
Total species			10	23	6	13	15	11

Aquatic insects of the study area listed in Table 4 will be referred to by their genus through the remainder of the thesis. References to other species not found in the study area will be referred to by species.

4.2.2 Aquatic Insect Distribution Between Lakes

Table 5 presents total abundance and percent total abundance for each taxon at the two lakes. Dominant taxa at Davey Lake were the mayfly Caenis punctata and the chironomid Dicrotendipes sp. The caddisfly Hydroptila ajax and the true bug Trichocorixa calva were also found in larger numbers. Taxa most abundant at Island Lake were the chironomids Tanytarsus sp., Chironomus sp., and Dicrotendipes sp. along with T. calva. The damselfly Ischnura perparva was common at both lakes, but more so at Island Lake. The Coleoptera as a group represented less than 1 percent of total abundance at each lake.

When abundance of a specific taxon was similar between lakes their percent contribution to the total abundance for each lake may be quite different. For example, numbers of Dicrotendipes and Trichocorixa were similar for both lakes but their percent contribution to the total is nearly 50 percent greater at Davey Lake than Island Lake.

Some taxa were much more abundant at one lake than the other. Tanytarsus represented 40.3 percent of the abundance

Table 5. Total abundance, and percent of total abundance per m² for aquatic insects at Davey and Island Lakes, Saguache County, Colorado, 1991.

Order Taxa	Davey L. (n=36)		Island L. (n=41)	
	Total	%	Total	%
Diptera				
Tipulidae	11	0.06	0	0
Anopheles	0	0	11	0.04
Culicoides	11	0.06	0	0
Tanypodinae*	334	2.0	840	3.5
Cricotopus	118	0.7	43	0.18
Chironomus	441	2.6	5242	21.9
Cryptochironomus	86	0.5	22	0.1
Dicrotendipes	4241	24.8	3886	16.2
Tanytarsus	388	2.3	9677	40.3
Dixa	0	0	140	0.58
Chrysops	11	0.06	0	0
Dolichopodidae	11	0.06	22	0.09
Ephydriidae	22	0.13	43	0.18
Scathophagidae	11	0.06	0	0
Hemiptera				
Hesperocorixa**	65	0.4	312	1.3
Trichocorixa	1647	9.6	1421	5.6
Ephemeroptera				
Callibaetis	65	0.4	237	1.0
Caenis	7072	41.3	248	1.0
Coleoptera				
Gyrinus	0	0	11	0.04
Haliphus	0	0	11	0.04
Celina	0	0	32	0.13
Hydroporus	11	0.06	0	0
Rhantus	0	0	22	0.09
Berosus	33	0.19	0	0
Staphylinidae				
Curculionidae	11	0.06	0	0
Odonata				
Anax	43	0.3	108	0.5
Ischnura	700	4.1	1658	6.9
Trichoptera				
Hydroptila	1701	9.9	0	0
Phryganea	32	0.19	0	0
Mystacides	22	0.13	0	0
Ocetis	11	0.06	0	0
Triaenodes	11	0.06	0	0

* Includes Larsia sp. and Procladius sp.

** includes some Sigara sp.

at Island Lake but only 2.3 percent at Davey Lake. Another example is Caenis which accounted for 41.3 percent of the abundance at Davey Lake and only 1 percent at Island Lake. Species richness (number of species) was greater at Davey Lake suggesting that the range of habitats was more diverse in these plots.

Table 6 presents the total dry weight (DW) biomass for taxa collected over the season. Taxa contributing greatest to biomass are similar to those with the abundance of individuals. Caenis, Ischnura, and the chironomids Chironomus and Dicrotendipes (Chironomini) were dominant at Davey Lake. The Odonata were dominant at Island Lake along with the chironomids Chironomus, Dicrotendipes, Tanytarsus, and the Hemiptera. Less numerous species such as Hesperocorixa laevigata and Anax junius were also dominant in biomass at Island Lake.

Similar biomass and percent contribution to total biomass for the Chironomini and Ischnura was seen between lakes. Tanytarsus represented 10.7 percent of the total biomass at Island Lake but only 0.6 percent at Davey Lake. Similar differences are seen with the Hemiptera, Caenis, and Anax. Comparing the abundance (Table 5) and biomass (Table 6) of Ischnura, Island Lake had nearly twice the number of individuals as Davey Lake yet the biomass was similar between lakes. This implies that the individual Ischnura

Table 6. Total dry weight biomass (mg), and percent of total biomass per m² for aquatic insects at Davey and Island Lakes, Saguache County, Colorado, 1991.

Order Taxa	Davey L. (n=36)		Island L. (n=41)	
	Total	%	Total	%
Diptera				
Tipulidae	10	0.2	0	0
Anopheles	0	0	1	0.1
Culicoides	12	0.2	0	0
Tanypodinae*	66	1.1	174	3.1
Cricotopus	13	0.2	13	0.2
Chironomini**	1291	22.6	1063	18.8
Tanytarsus	37	0.6	603	10.7
Dixa	0	0	19	0.3
Chrysops	37	0.6	0	0
Dolichopodidae	12	0.2	24	0.4
Ephydriidae	17	0.3	68	1.2
Scathophagidae	16	0.3	0	0
Hemiptera				
Hesperocorixa***	199	3.5	413	7.3
Trichocorixa	181	3.2	593	10.5
Ephemeroptera				
Callibaetis	115	2.0	187	3.3
Caenis	1480	25.9	34	0.6
Coleoptera				
Gyrinus	0	0	14	0.2
Haliphus	0	0	7	0.1
Celina	0	0	26	0.5
Hydroporus	8	0.1	0	0
Rhantus	0	0	23	0.4
Berosus	36	0.6	0	0
Staphylinidae				
Curculionidae	17	0.3	0	0
Odonata				
Anax	10	0.2	1001	17.7
Ischnura	1314	23.0	1376	24.4
Trichoptera				
Hydroptila	579	10.1	0	0
Phryganea	210	3.7	0	0
Mystacides	34	0.6	0	0
Ocetis	5	0.1	0	0
Triaenodes	4	0.1	0	0

* Includes Largia sp. and Procladius sp.

** Includes Chironomus sp., Dicrotendipes sp., and Cryptochironomus sp.

*** Includes Sigara sp.

were larger at Davey Lake. Presence of vegetation, environmental conditions or availability of prey may have had role in determining these distributions.

Mean weight per individual for each taxon over the sampling season is presented in Table 7. Individuals of dominant taxa such as the Chironomini, Tanytarsus and Trichocorixa along with Caenis and Ischnura occurred over the entire season at the lakes. Of these, Ischnura and Caenis had larger individual weights and were more abundant in terms of abundance (Table 5). Caenis, however, was abundant only at Davey Lake where as Ischnura had many individuals at each lake. The smaller larvae of Chironomini were more abundant at both lakes. Other taxa that produced heavier individuals were Anax, Hesperocorixa, the Coleoptera, and the Trichoptera. These taxa, however, had lower numbers of individuals, were present later or infrequently through the season, or were present at only one of the lakes. Highest mean individual weight for many taxa was seen in July and October. This could be related to phenology as many taxa may be emerging into adults at this time. Lower individual weights in August may be from hatching of eggs producing more individuals as seen by the Chironomini and Ischnura.

From the data in Table 7 life history attributes can be detected. For example, Ischnura had larger size classes

Table 7. Mean weight (mg) per individual for aquatic insects at Davey and Island Lakes, Saguache County, Colorado, 1991.

Order Taxa	29 May	15 June	19 July	23 Aug	18 Sept	21 Oct
Diptera						
Tipulidae	0	0	0	0	0.90	0
Anopheles	0	0	0	0.1	0	0
Culiciodes	0	1.10	0	0	0	0
Tanypodinae*	0	0.30	0.16	0.35	0.22	0.24
Cricotopus	0	0.10	0.30	0.23	0.38	0
Chironomini**	0.26	0.15	0.11	0.16	0.11	0.17
Tanytarsus	0.10	0.08	0.22	0.07	0.11	0.08
Dixa	0	0	0.15	0.27	0.19	0.20
Chrysops	0	3.40	0	0	0	0
Dolichopodidae	1.10	0	0	0	0	0
Ephydriidae	1.00	0	0	1.23	0	0.98
Scathophagidae	0	0	0	0	0	0.50
Hemiptera						
Hesperocorixa***	0	0	0.60	0.49	3.09	2.00
Trichocorixa	0.20	0.07	0.51	0.37	0.42	0.41
Ephemeroptera						
Callibaetis	0	0	0.90	2.01	0.07	0.41
Caenis	0.20	0.24	0.21	0.12	0.08	0.16
Coleoptera						
Gyrinus	0	0	14.00	0	0	0
Haliphus	0	0	0	0.60	0	0
Celina	0	0.20	0	1.33	0	0
Hydroporus	0	0	0.70	0	0	0
Rhantus	0	0	0	0	0	1.05
Berosus	1.20	0	0	0	0	0
Staphylinidae	0	0	0	0	1.10	0
Curculionidae	0	1.6	0	0	0	0
Odonata						
Anax	0	0	1.80	4.28	4.63	15.83
Ischnura	2.65	2.61	3.13	0.38	0.55	0.82
Trichoptera						
Hydroptila	0.38	0.25	0	0.19	0	0
Phryganea	0	0	0	1.0	0	17.50
Mystacides	2.70	0	0.50	0	0	0
Ocetis	0	0.5	0	0	0	0
Triaenodes	0.40	0	0	0	0	0

* Includes Larsia sp. and Procladius sp.

** Includes Chironomus sp., Cryptochironomus sp. and Dicrotendipes sp.

*** Includes Sigara sp.

occurring in July and the smaller individuals in August. This suggests that Ischnura had one generation per year and that adult emergence occurred some time in July. Other taxa are not so clear due to the small range of individual weights and the possibility of several age classes being present at the same time. Individual mean weights from Table 7 used with abundance figures of Table 5 may provide information on what species may be important with respect to quantity of food available for waterfowl at a particular time for the area.

Mean monthly abundance for all aquatic insects from 29 May to 21 October at Davey and Island Lakes is presented in Figure 5. In May Davey Lake had the highest mean abundance where Island Lake was at its lowest mean abundance. In July Davey Lake was at its lowest mean abundance where Island Lake was at its greatest abundance. Both Lakes had increases in abundance from September to October.

Mean biomass for all aquatic insects from 29 May through 19 October is presented in Figure 6. Davey Lake is highest in biomass in May and decreases through September. Island Lake has the lowest biomass in May and increases through September. Both lakes increase in biomass for September through October.

Life cycles of aquatic insects may play a role in abundance and biomass distributions. Abundance peaks may be

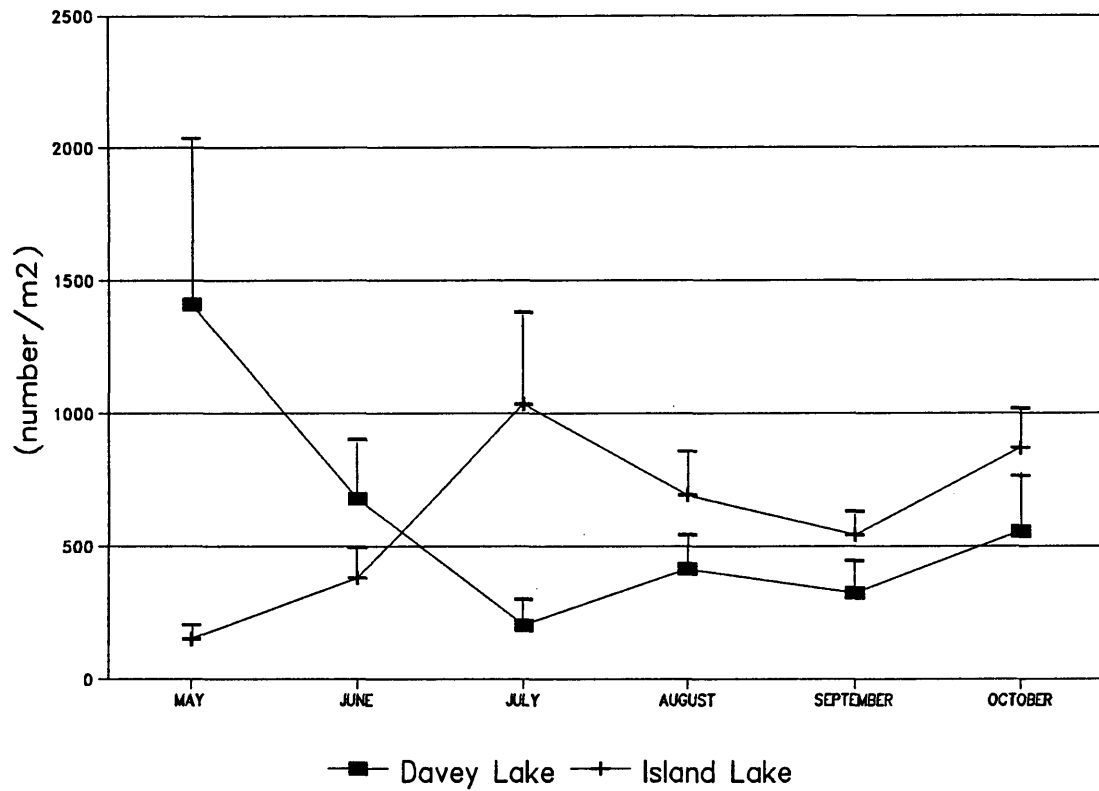


Figure 5. Mean monthly abundance (number/m²) of aquatic insects at Davey and Island Lakes, Russell Lakes Wildlife Area, Saguache County, Colorado, 1991. Error bars indicate standard error.

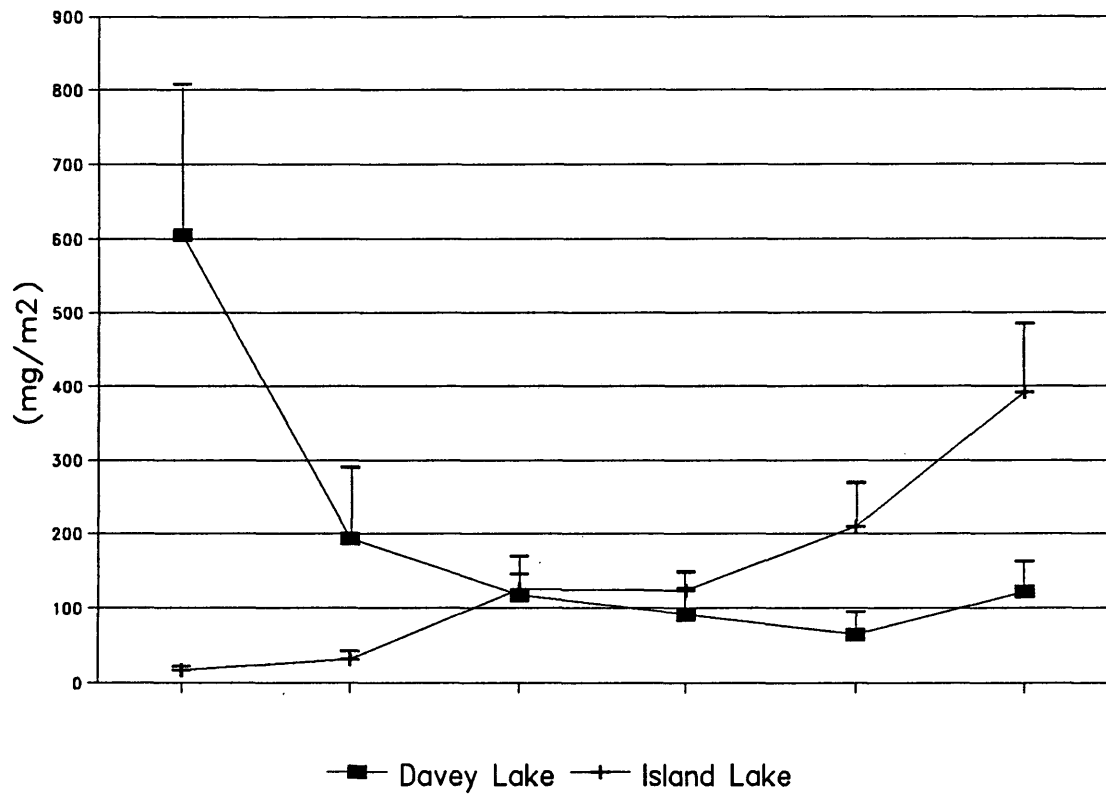


Figure 6. Mean monthly biomass (mg/m²) for aquatic insects at Davey and Island Lakes, Russell Lakes Wildlife Area, Saguache County, Colorado, 1991. Error bars indicate standard error.

due to recruitment of new individuals and declines by adult emergence. This is evident in Table 7 where more abundant taxa such as the Chironomini had low individual weights in July and Caenis, and Ischnura had lower mean individual biomass in August. Predation may have also caused declines, particularly in the Chironomidae. Chironomid larvae are often the major component of the diet of Ischnura (Thompson 1978). Dicrotendipes were particularly abundant at lakes providing possible prey for Ischnura. As a percentage of total abundance, higher values of Ischnura at Island Lake corresponded to lower values of Dicrotendipes where the reverse was true at Davey Lake (Table 3) indicating that as predators abundance increase prey abundance decreases.

4.2.3 Distribution of Aquatic Insects in Community Plots

For all communities species richness (number of species present) was greatest in the bulrush community at Davey Lake with 23 different taxa being identified (Figure 7). At Island Lake the bulrush community had the greatest species richness with 15 different taxa. Lowest species richness for both lakes was seen in the sedge communities with Davey and Island Lake having 6 and 12 taxa, respectively.

Both sedge communities will be considered in general terms with respect to number of species per sample,

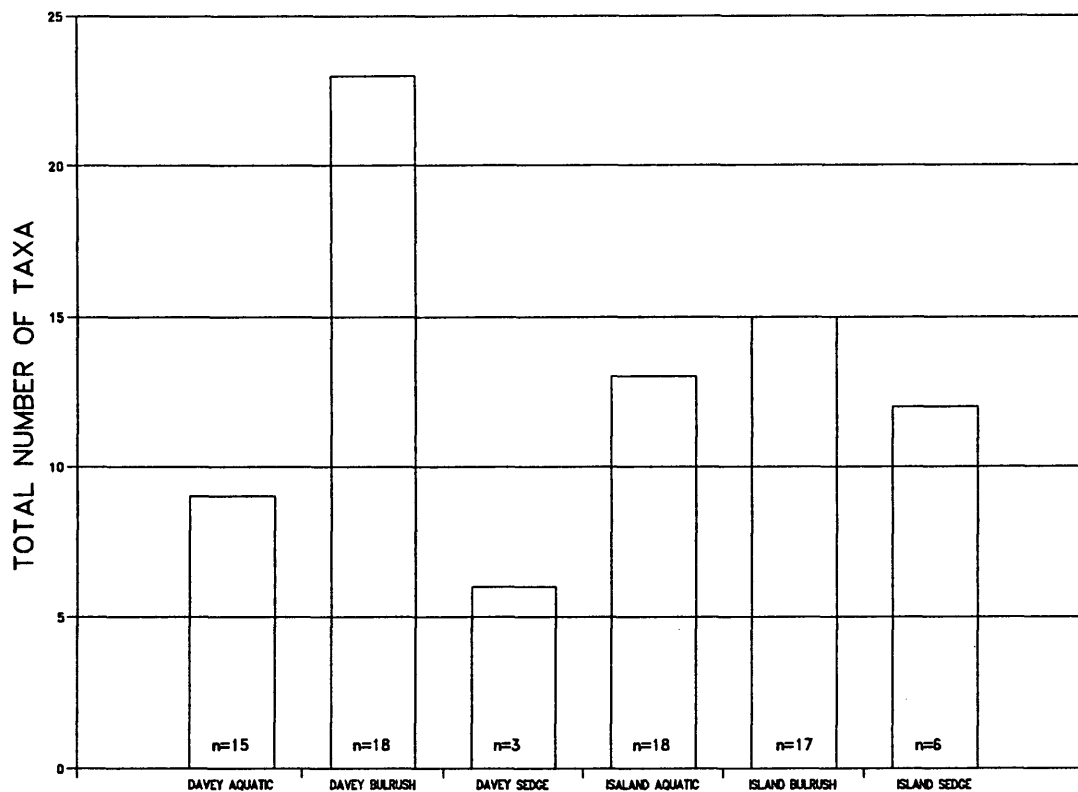


Figure 7. Total number of aquatic insect taxa in each community at Davey and Island Lakes, Russell Lakes Wildlife Area, Saguache County, Colorado. n = total number of samples collected from 29 May to 21 October, 1991.

abundance and biomass but will not be compared statistically to other communities due to their small sample size.

Mean numbers of taxa collected in each sample for each community is presented in Table 8. The bulrush community at Davey Lake showed the highest mean number of taxa per sample but is not significantly different than the bulrush community of Island Lake ($P > 0.05$). The aquatic communities were significantly different between Lakes in the mean number of taxa per sample ($P < 0.05$). A significant difference in mean number of taxa per sample was seen between the aquatic and bulrush communities at Davey Lake but no significant difference was seen between the bulrush and aquatic communities at Island Lake ($P > 0.05$).

Mean abundance of aquatic insects was highest in the bulrush community and lowest in the sedge community at Davey Lake (Figure 8). Comparison of abundance in the bulrush and aquatic communities within lakes show that at Davey Lake differences were significant ($P < 0.05$) where Island Lake differences were not significant ($P > 0.05$). Between lakes the abundance of aquatic insects was significantly different between aquatic communities ($P < 0.05$) but not significant in bulrush communities ($P > 0.05$).

Mean biomass was highest in the bulrush community at Davey Lake and lowest at the sedge community at Davey Lake (Figure 9). At Davey Lake the bulrush and aquatic

Table 8. Number of samples, mean number of taxa collected in each sample, standard error and minimum and maximum number of taxa for samples for each community at Davey and Island Lakes, Russell Lakes Wildlife Area, Saguache County, Colorado, 29 May - 21 October, 1991.

Community	Number of samples	Mean number of taxa	Standard error	Min.-Max.
Davey Lake				
aquatic	15	3.7	0.40	2-7
bulrush	18	6.3	0.58	3-11
sedge	3	2.0	1.53	0-5
Island Lake				
aquatic	18	5.4	0.55	2-9
bulrush	17	5.4	0.58	2-10
sedge	6	2.2	0.98	0-6

communities were significantly different in mean biomass ($P < 0.05$) while at Island Lake differences in biomass were not significant ($P > 0.05$). Between lakes the bulrush communities were not significantly different ($P > 0.05$) in mean biomass but the aquatic communities were significantly different ($P < 0.05$).

The higher number of taxa in the bulrush community at Davey Lake suggests that more available habitat was present there to support a wider range of aquatic insects. Lower standing crop of aquatic vegetation in the aquatic community at Davey Lake likely is the reason for lower

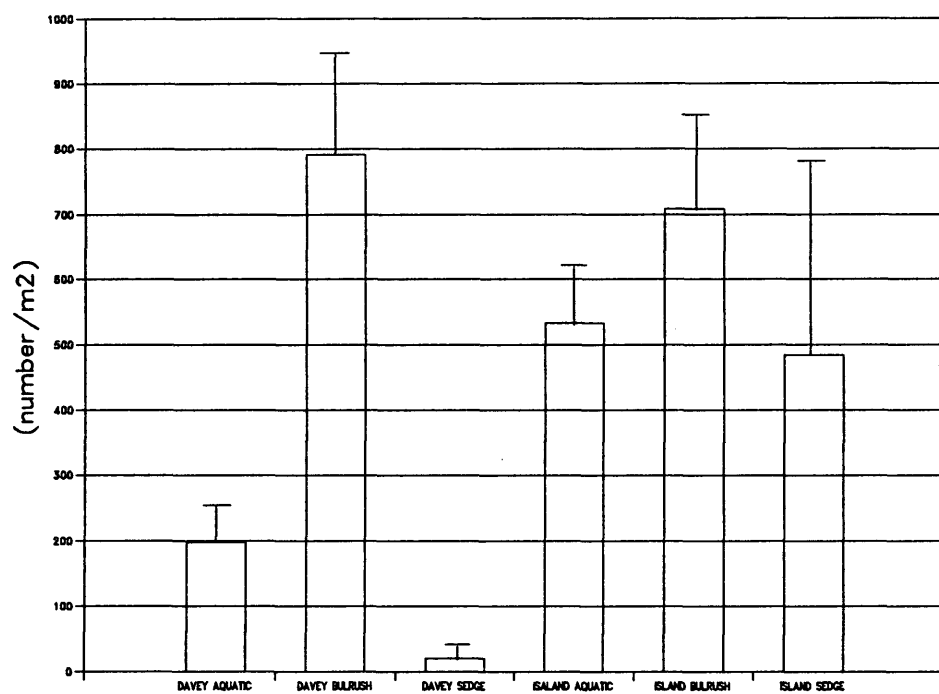


Figure 8. Mean abundance (number/m²) for communities at Davey and Island Lake, Saguache County, Colorado, 19 May - 21 October, 1991.

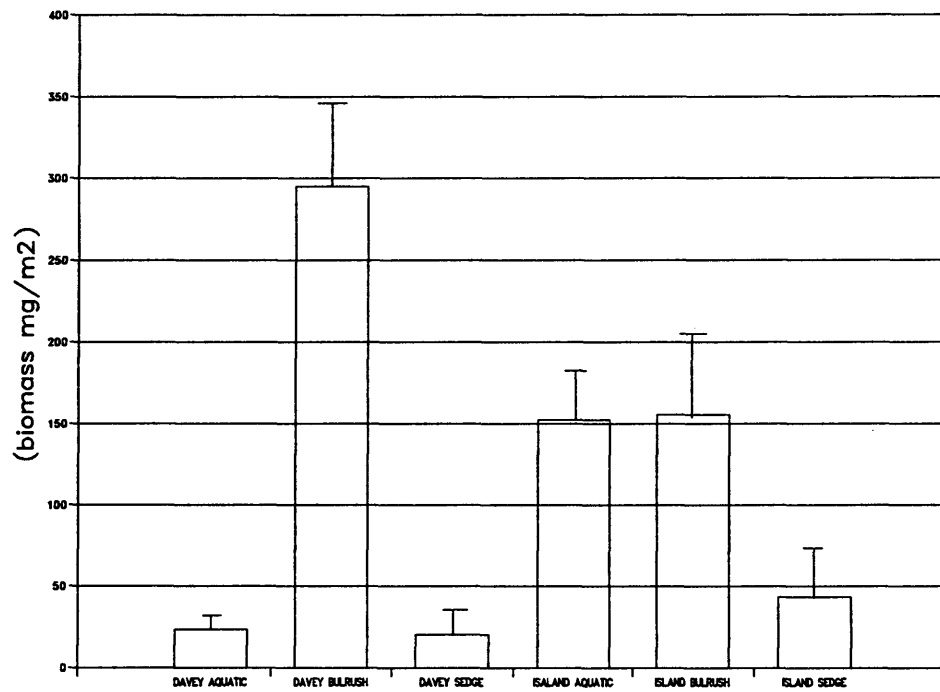


Figure 9. Mean biomass (mg/m²) for aquatic insects at the communities at Davey and Island Lakes, Russell Lakes Wildlife Area, Saguache County, Colorado, 19 May - 21 October, 1991.

species richness.

Monthly mean abundance of aquatic insects in the three communities for Davey and Island Lakes is presented in Figures 10 and 11, respectively. At Davey Lake the highest abundance for the bulrush and aquatic community plots was seen in May and June, respectively. The sedge community plot of Davey Lake was sampled once in September and had comparatively low numbers. At Island Lake highest numbers for the aquatic, bulrush and sedge community plots was seen in June, July and August, respectively. In May the bulrush community plot at Davey Lake had the highest overall abundance for the sampling period compared to the other plots at Davey Lake. The highest abundance for Island Lake for the sampling period also occurred in the bulrush community plot buy in July. Lowest abundance for the aquatic and bulrush community plots at Davey Lake occurred in July and September, respectively. For Island Lake lowest numbers occurred in May for both the aquatic and bulrush community plots and in June for the sedge plot.

Bulrush community plots at the two lakes were similar in abundance from August through October. The aquatic and bulrush community plots at both lakes showed a large increase in abundance from September to October. At Island Lake the sedge community plot had very low abundance in

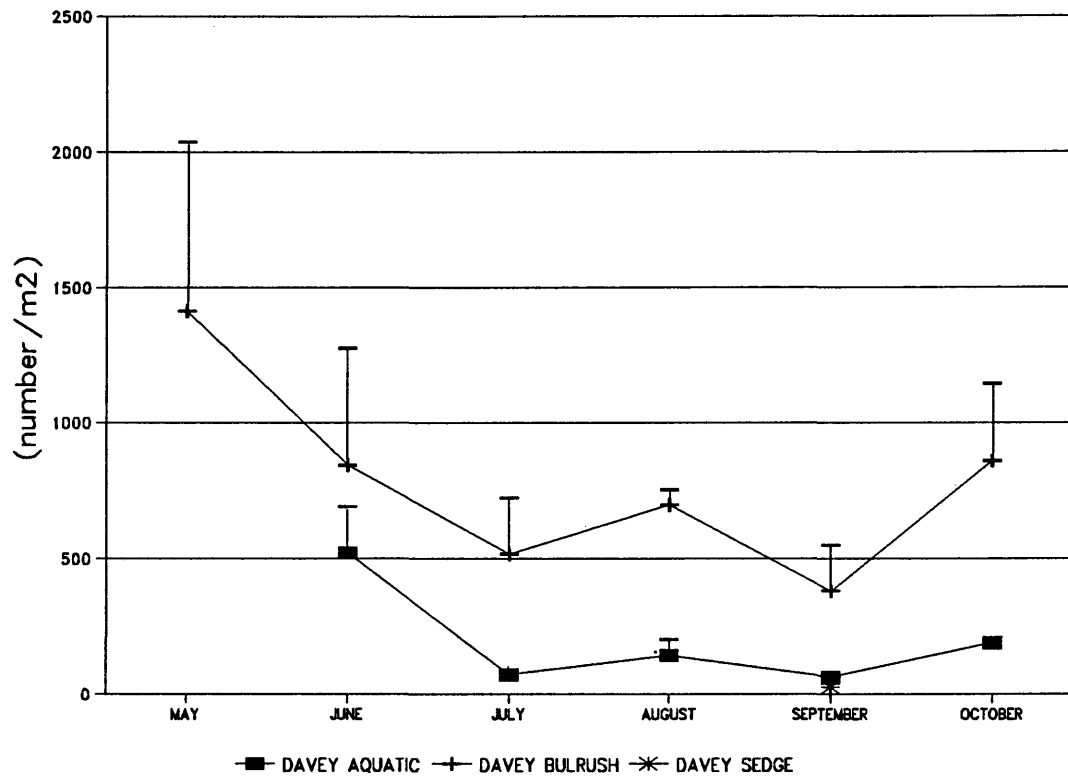


Figure 10. Mean monthly abundance (number/m²) of aquatic insects at the community plots at Davey Lake, Russell Lakes Wildlife Area, Saguache County, Colorado, 1991. Error bars indicate standard error.

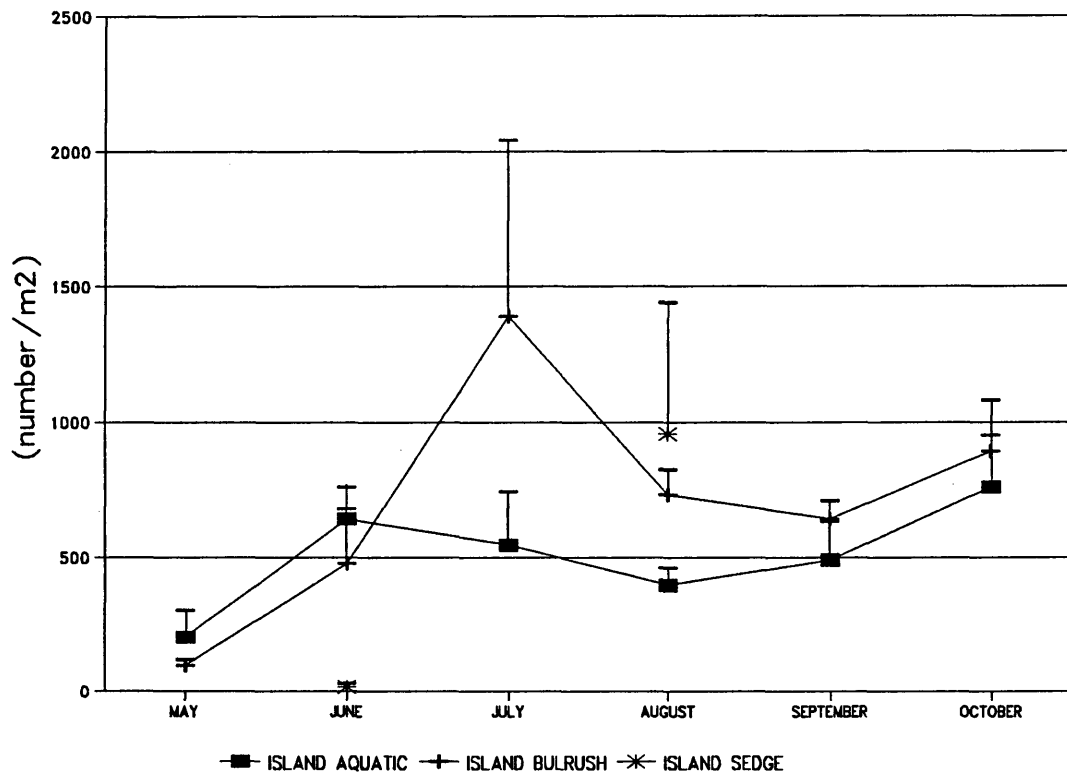


Figure 11. Mean monthly abundance (number/m²) of aquatic insects at Island Lake at Russell Lakes Wildlife Area, Saguache County, Colorado, 1991. Error bars indicate standard error.

June, but when sampled again in August, aquatic insects abundance was much higher. The sedge community at Davey Lake was sampled only in September and numbers were low then.

Community mean abundance is greatest in the bulrush community at Davey Lake. The least number of individuals was in the sedge community at Davey Lake. At Island Lake the bulrush community had more individuals than the aquatic. The sedge community at Island Lake had a sizable number of individuals compared to that of the sedge community at Davey Lake.

The order of community mean abundance in Figures 10 and 11 corresponds to the order of species richness for communities in Table 4 and Figure 7. The bulrush community of Davey Lake displayed highest numbers for both abundance and species richness whereas the sedge community at Davey Lake had both the lowest abundance and species richness. This would indicate that the habitat was more complex and/or environmental conditions were more suitable in the bulrush community at Davey Lake for supporting aquatic insects. The combination of the aquatic vegetation and the higher quantities of coarse particulate organic matter may be the reason for these higher numbers. Conversely, the sedge plot at Island Lake was flooded periodically through the season possibly affecting the distribution of aquatic insects.

Opportunity for egg laying and hatching by species favoring shallow water would be greater in the flooded sedge community. The shallow water would also be warmer promoting greater activity and growth in aquatic insects (Sweeny 1984). The aquatic community of Davey Lake had very little vegetation and lacked the accumulation of coarse organic matter. This provided little available habitat for aquatic insects which probably accounted for the relatively low abundance and species richness.

Mean monthly biomass for the three community plots at Davey and Island Lakes is presented in Figures 12 and 13. The aquatic plot at Davey Lake had low biomass through the season, never reaching the levels of the other plots. Biomass at the bulrush plot of Davey Lake generally followed the same pattern as abundance, with a maximum in May and a low in September. Aquatic and bulrush plots at Island Lake had continuous increases in biomass over the season. The bulrush plots of both lakes had a large increase in biomass from September to October, especially at Island Lake, which corresponds to the increase in abundance seen in Figures 10 and 11.

Monthly mean biomass for Davey Lake in Figure 12 shows a decrease in biomass through the season with a substantial increase in October. Conversely, Island Lake (Figure 13) shows an increase through the season with a significant rise

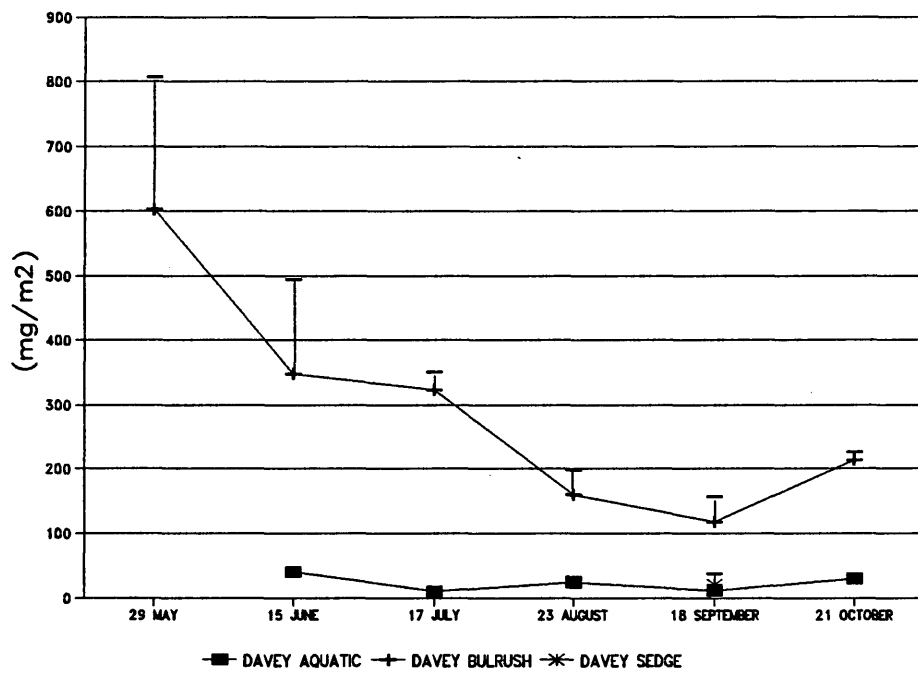


Figure 12. Mean monthly biomass (mg/m^2) of aquatic insects at three communities at Davey Lake, Russell Lakes Wildlife Area, Saguache County, Colorado, 1991. Error bars indicate standard error.

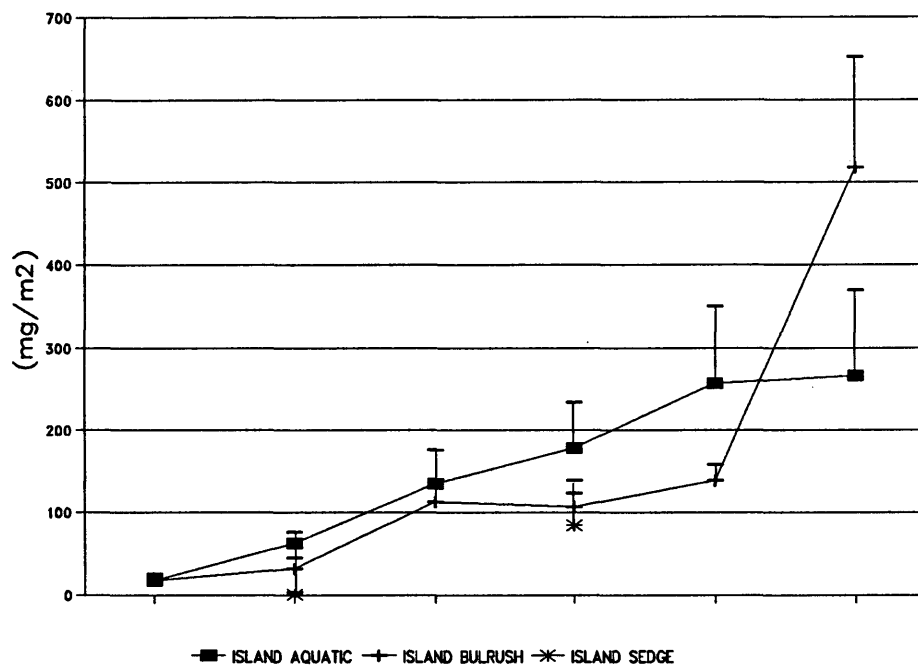


Figure 13. Mean monthly biomass (mg/m²) of aquatic insects in three communities at Island Lake, Russell Lakes Wildlife Area, Saguache County, Colorado, 1991. Error bars indicate standard error.

in biomass again in October. These patterns are well represented in the corresponding bulrush community plots at each lake. The reason for this may be that Caenis, the dominant taxa in abundance and biomass at Davey Lake (Tables 5 and 6), appear to emerge as adults in August (Table 7). Adult emergence of Ischnura also appears to occur at this time adding to the loss in biomass. With the emergence of these two taxa a substantial portion of the relative abundance and biomass of Davey Lake is lost. The smaller Chironomidae, which makeup a smaller percentage of the total biomass, dominated at this time. Island Lake had larger taxa contributing greater percentages to total biomass, maintaining levels over the season.

The bulrush plot at Davey lake was the most important for early biomass production. Biomass in May was the highest of any of the sampled communities. The aquatic and bulrush community plot at Island Lake are important later in the season, especially the bulrush plot in October. The importance of the bulrush communities in the production of aquatic insect biomass can be attributed to the increased complexity of the environment. This complexity is from the different forms of vegetation (both bulrush and submerged aquatic plants), and additionally at Davey Lake, the CPOM.

A comparison of the abundance and biomass of aquatic insects in the RLWLA to other wetlands where similar studies

have been conducted is presented in Table 9. In general the RLWLA had lower abundance and biomass of aquatic insects. The greatest mean values for abundance of aquatic insects at RLWLA was for the bulrush community plot at Davey Lake having a mean of 784 individuals per m^2 over the months of May through September, 1991 (Figure 5). Ranges in abundance at RLWLA were from 30 per m^2 at the sedge plot at Davey Lake in September to 1414 per m^2 in the bulrush plot at Davey Lake in May. Community abundance and biomass levels are much lower than other studies listed in Table 9. Maximum mean monthly biomass at the RLWLA study plots was 301 mg/m^2 (Figure 6) at the bulrush plot of Davey Lake with ranges of 10 to 604 mg/m^2 at the aquatic and bulrush plots at Davey Lake, respectively. The low biomass may reflect environmental conditions of the region, such as higher pH, a short growing season or other factors not addressed.

Water levels in the lakes over the past may also have a role in the low productivity of aquatic insects. Water levels that are maintained at high levels over extended periods of time can tie up nutrients in the sediments. In North Dakota, greater numbers of waterfowl were found to use temporary wetlands due to the frequent drawdown and release of nutrients, promoting aquatic invertebrate population (Kantrund and Stewart 1977).

Standing crop for the bulrush community plots should

Table 9. Abundance and biomass estimates of other studies in wetland communities compared to estimates in the Russell Lakes Wildlife Area, Saguache County, Colorado, 1991.

Site	Abundance	Biomass	Study
Lizard Lake, Pocahontus County, Iowa			
-wooded shore 30-45 cm water depth	4108/m ²	1297 mg/m ²	Tebo (1955)
-shore line 30-45 cm water depth	3856/m ²	671 mg/m ²	
-heavily vegetated shallow bay 45-60 cm water depth	3497/m ²	1846 mg/m ²	
Lake Erie, United States			
Chironomid larvae			
-Potamogeton	3000/yard ²		Krecker & Lancaster (1939)
-Chlodophoria	7500/yard ²		
-Scirpus	19000/yard ²		
Canadian subarctic			
Chironomid larvae			
-shallow eutrophic bay	1500/m ²		Moore (1980)
Lake Vechten, Nederlands			
Invertebrates			
-dead Typha		5.23g/m ₂	Dvorak & Best (1982)
-Polygonum, Phragmites, Ceratophyllum		1.41-4.35g/m ²	
-Sparganium, Polygonum, Elodea, Nitella		0.58-1.67g/m ₂	
RLWLA, Colorado			
-bulrush community	784/m ²	301mg/m ²	(this study)

not be limiting to the production of aquatic insects. A comparison of bulrush standing crop to that of other similar wetland of the United States found production to be similar (Cooper and Severn 1991).

4.3 Detrended Correspondence Analysis of Plots

Detrended Correspondence Analysis (DCA) the individual communities show dispersion along both axis 1 and axis 2 (Figure 14). This graph was generated using species composition and abundance of each stand. The stands for the sedge community plot at Davey Lake were deleted from this analysis because the taxa representing this plot, Berosus sp., Tipulidae, Dolichopodidae, and Scathophagidae, were unique to stands of this plot, and only one chironomid specimen was collected in the samples. The discontinuity of this data made the DCA analysis impossible.

The range of stand scores for axis 1 (representing standard deviations) are from approximately -1.7 to +3.4 for a total of 5.1 standard deviations. Axis 2 stand scores range from -0.9 to +4.1 for a total of 5.0 standard deviations. Stands having a difference greater than 4 standard deviations would have very little faunistic similarity (Jongman et al. 1987). The eigenvalue (a measure of maximum dispersion or importance of the ordination axis) for axis 1 is much larger than axis 2, showing factors which control species composition and abundance along axis 1 have a greater influence than those controlling axis 2. Eigenvalues greater than 0.5 show that taxa are well separated along the axes (Jongman et al. 1987).

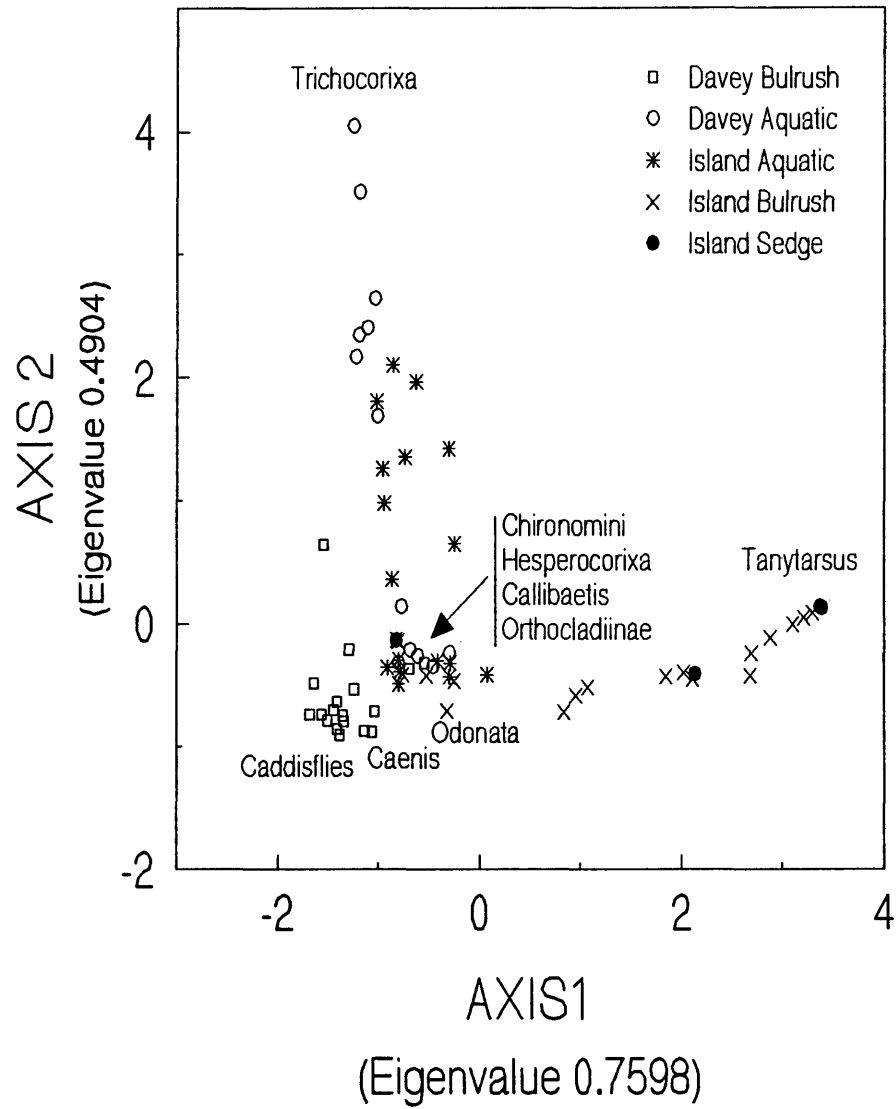


Figure 14. DCA ordination diagram for aquatic insect samples at Davey and Island Lakes, Saguache County, Colorado, 1991. Arrow points to location in diagram of four taxa.

The sedge and bulrush community plots at Island Lake each had a dispersion of nearly 4 standard deviations along axis 1. This indicates that in these two communities the fauna in the stands at each extreme of the dispersions of were dissimilar. Included were many rare species with low abundance thus accounting for the large range in stand scores in these communities. The remaining plots had similar dispersion along the first axis of nearly one standard deviation indicating more similarity in sample abundance and the taxa present in each sample stand. The bulrush community of Davey Lake has a distribution of about 1 standard deviation along axis 1 showing greater taxa commonality among the sample stands. This could be related to the differences in the complexity of the plots, being that Davey Lake has a more CPOM than Island Lake.

Greatest dispersion along axis 2 was seen in the aquatic communities of both lakes, being 4.4 and 2.6 standard deviations for Davey and Island Lakes, respectively. The least dispersion along axis 2 was 0.54 standard deviations in the sedge plot at Island Lake.

Several taxa have an influence on the magnitude and direction of the ordination. At the center of the ordination diagram are the more common taxa such as the Chironomini, Tanypodinae, Orthocaldiinae, Hesperocorixa, and Callibaetis. Many times these taxa would likely be present

in samples less than 4 standard deviations away from their location on their ordination diagram. All plots converge near the points represented by these taxa.

A second grouping of taxa is seen at -2.00 on axis 1 indicating their maximum abundance in the bulrush community of Davey Lake. Taxa at this region on the diagram are the caddisflies Phryganea, Hydroptila, Triaenodes, Oecetis and Mystacides along with Caenis and some less abundant taxa. With the exception of Hydroptila, these caddisflies make their cases from plant fragments. Many of the stand samples in this plot contained relatively large amounts of coarse particulate organic matter which provided case building material for these caddisflies. Caenis is also associated with this group and was a major taxon at Davey Lake. Caenis has a large pair of protective operculate gill covers enabling it to feed in the detritus beds of Davey Lake. Studies by Williams and Hynes (1974) found Caenis regularly at depths to 40 cm in the substratum of a creek . Hydroptila's association with this group in the bulrush community plot of Davey Lake is its preference for stems of the bulrush to which it attaches its case which is made of silk and fine mineral material. Hydroptila was only found on the bulrush at Davey Lake, due possibly to decreased stem density found there. A response to greater light intensity may explain the presence of Hydroptila. Certain mayflies

and caddisflies have been found to favor certain light intensities when all other environmental factors are similar (Minshall 1984).

The odonates, Ischnura and Anax, were found in close association with the bulrush plots at both lakes and the aquatic plot of Island Lake. These plots had the greatest amount of aquatic vegetation which Ischnura and Anax, as climbers (Table 2), prefer for stalking prey.

Tanytarsus were strongly associated with the sedge and bulrush plots at Island Lake, both numerically and as indicated by presence in many samples. Tanytarsus appeared to have been associated with shallow water habitats associated with the bulrush and sedge community plots of Island Lake. These two plots had shallow standing water depths. Cantrell and McLachlan (1977) found that Tanytarsus gregarius (Kieffer) was closely associated with lake margins and showed a marked phototaxis. Tanytarsus in the study area may respond in the same manner.

Trichocorixa was strongly associated with the aquatic plot at Davey Lake and to a lesser degree with the aquatic plot at Island Lake. This may indicate that Trichocorixa associates with deeper water, particularly areas with low vegetation biomass such as the aquatic community plot of Davey Lake.

Samples were collected over a six month period so the

ordination diagram also reflects temporal changes in composition and abundance of aquatic insects. Stands sampled in October are near zero on both axes, close to the central group of species mentioned previously. Many of these taxa are chironomids, showing that this may be the primary group that over-winter as larvae and nymphs in these communities. The progressive temporal pattern in the bulrush plot at Island Lake has samples reaching higher axis 1 values in July, then converging back to near zero in October. The higher axis 1 values are associated with Tanytarsus. The pattern seen along axis 2 for the aquatic plot at Davey Lake reached maximum values in June and August, but again is near zero in October. Trichocorixa is associated with the higher axis 2 values.

Sample scores for the four DCA axes were correlated to vegetation and environmental variables using Spearman rank correlation (Table 10). A negative correlation to water depth was seen for axis 1 indicating that as values for axis 1 increase water depth decreases. Tanytarsus was the taxon that responded greatest to this variable along axis 1, being found in more shallow water particularly the sedge community at Island Lake. Positive correlation of axis 1 to the density of live bulrush stems was also seen. As stand scores increase so does bulrush stem density. Hydroptila responded to this variable being present only in the less

Table 10. Spearman rank coefficients (100 x r) and levels of significance for environmental variables for the first four DCA axes.

Variable	axis 1		axis 2		axis 3		axis 4	
	r	Sig.level	r	Sig.level	r	Sig.level	r	Sig.level
water depth	-37	0.0022	37	0.0026	-3	0.8071	3	0.8308
detritus thickness	-34	0.0154	11	0.4276	-15	0.2688	3	0.8486
water temperature	22	0.0825	-11	0.4018	-4	0.7393	-7	0.6040
live bulrush density	63	0.0040	32	0.1418	60	0.0060	-35	0.1117
time (month)	-6	0.6075	-9	0.4543	13	0.2936	22	0.0647
eigenvalue	0.75980		0.4904		0.27166		0.16246	

dense bulrush of Davey Lake. Axis 2 showed a positive correlation to water depth which explains the distribution of the aquatic and bulrush communities at each lake with Davey Lake generally having deeper depth than Island Lake. Trichocorixa responded to this variable generally increasing its presence in the deeper water of the aquatic plot of Davey Lake.

4.4 Distribution of Functional Groups in Wetland Communities in the Study Area

Of the six functional groups presented in Table 1, four were represented in the study plots at RLWLA. These groups are the collectors, predators, shredders, and the macrophyte piercers. Scrapers and parasites were not found in the

sample stands. The absence of scrapers could be an indication that benthic periphyton, the primary food of scrapers, is limiting.

4.4.1 Functional Groups in the Aquatic Communities

Collectors, predators and macrophyte piercers were present at Davey Lake with five, three and one taxa representing each group, respectively (from Table 2). Island Lake had 6 collector taxa, 5 predators, and macrophyte piercers and shredders one each.

Predators were the most abundant in the aquatic community at Davey Lake while collectors dominated this community at Island Lake (Table 11). In the aquatic community at Davey Lake predators were nearly twice as abundant as collectors in the aquatic community. At Island Lake collector abundance was more than double that of predators. As noted earlier smaller instar predators are many times omnivorous and do not exclusively consume live prey when in these stages possibly accounting for the greater number of predators. Between lakes, collectors were more than four times as abundant at Island Lake as at Davey Lake where predators at Island Lake were nearly 20 percent more abundant than Davey Lake in the aquatic community plot. Macrophyte piercers and shredders contributed had low abundance at Island Lake and macrophyte piercers presented

Table 11. Mean abundance per m² and standard errors (S.E.) for functional groups of all aquatic insects in the six communities at Russell Lakes Wildlife Area, Saguache County, Colorado, 1991.

	Collectors		Predators		Piercers		Shredders	
	Mean	(S.E.)	Mean	(S.E.)	Mean	(S.E.)	Mean	(S.E.)
Davey Lake								
aquatic	74.6	(5.3)	121.3	(13.8)	0.7	(0.4)	0	0
bulrush	617.7	(41.3)	58.0	(3.4)	98.1	(34.2)	9.6	(1.5)
sedge	3.6	(1.2)	7.2	(1.3)	7.2	(2.4)	7.2	(2.0)
total	695.9		186.5		106.0		16.8	
Island Lake								
aquatic	334.3	(23.9)	151.3	(9.1)	16.2	(3.6)	2.4	(0.6)
bulrush	624.3	(59.5)	81.7	(6.4)	1.3	(0.4)	0.1	(0.1)
sedge	713.1	(161.2)	5.4	(1.0)	2.7	(1.4)	0	0
total	1671.7		238.4		20.2		2.4	

had low abundance at Davey Lake with shredders lacking there.

Biomass in the aquatic community at Davey Lake was nearly equally represented by collectors and predators where at Island Lake, predators had nearly double the biomass as collectors (Table 12). Between lakes, collectors at Island Lake had more than four times the biomass as Davey Lake and predators had nearly eight times more biomass at Island Lake. Macrophyte piercers biomass was most prevalent in the aquatic community at Island Lake with comparatively low biomass at Davey Lake. Macrophyte piercer biomass at both lakes was relatively low when compared to the other functional groups. Shredders were not present at levels

Table 12. Mean biomass (mg/m²) and standard errors for functional groups of all aquatic insects in the six communities at Russell Lakes Wildlife Area, Saguache County, Colorado, 1991.

	Collectors		Predators		Piercers		Shredders	
	Mean	(S.E.)	Mean	(S.E.)	Mean	(S.E.)	Mean	(S.E.)
Davey Lake								
aquatic	10.6	(1.3)	11.7	(0.9)	0.5	(0.3)	0	0
bulrush	156.4	(11.1)	81.1	(6.2)	43.5	(13.6)	13.6	(4.3)
sedge	0.7	(0.2)	7.2	(1.3)	7.5	(2.5)	8.6	(2.5)
total	167.7		100.0		51.5		22.2	
Island Lake								
aquatic	45.9	(3.8)	83.6	(6.2)	22.4	(6.0)	0.72	(0.2)
bulrush	54.1	(4.9)	100.2	(8.5)	0.8	(0.3)	0.13	(0.1)
sedge	57.6	(10.8)	5.9	(1.4)	0.8	(0.4)	0	0
total	157.6		189.7		24.0		2.4	

greater than 2 percent abundance or biomass at Davey Lake in the aquatic community but were present at Island Lake in comparatively low biomass to the other groups. Dominance in biomass by predators at Island Lake may be due to the increased complexity of the habitat provided by vegetation. This would tend to support greater numbers of taxa and individuals, providing more prey for predators, in this case Ischnura.

4.4.2 Functional Groups in the Bulrush Communities

Four functional feeding groups occurred at each lake in the bulrush community. Collectors were represented by seven taxa at each lake. Nine predators taxa were at Davey Lake

while at Island Lake, six taxa were present. Three macrophyte piercer taxa are present at Davey Lake and two at Island Lake. Four taxa representing the shredders were at Davey Lake with one at Island Lake.

In the bulrush community at both lakes, collectors in general were the most abundant over all other functional groups (Table 11). Macrophyte piercers were second in abundance at Davey Lake, where as at Island Lake, predators were second in abundance. Shredder abundance in the bulrush community at Davey Lake was much greater than at Island Lake with both lakes being relatively low in abundance compared to the other functional groups.

Biomass in the bulrush community at Davey Lake was dominated by collectors while at Island Lake predators dominated (Table 12). Predators had nearly half the biomass as collectors at Davey Lake and double the biomass at Island Lake. Macrophyte piercers and shredders at Davey Lake had respectable weights but biomass was small at Island Lake for the two groups.

Communities where collectors dominated biomass may indicate that sufficient FPOM is present to support these populations. Predators are likely to have higher biomass in communities that have sufficient prey. Macrophyte piercers appear to be more closely associated with the bulrush communities indicating a relationship to the bulrush.

Communities where shredders exhibit greater biomass may indicate that sufficient coarse plant material is present to support these populations.

4.4.3 Functional Groups in the Sedge Communities

All four functional groups were represented at Davey Lake with three being represented at Island Lake, the shredders lacking. At Davey Lake collectors and shredders were represented by two taxa each and one taxa each represented predators and macrophyte piercers. For Island Lake, collectors had six taxa, predators had five taxa with one taxa for macrophyte piercers.

Abundance at Davey Lake was dominated equally by predators, macrophyte piercers and shredders, all having very low numbers compared to other communities (Table 11). Island Lake was dominated by collectors in numbers greater than those of any other community. Numbers of the other functional groups at Island Lake were relatively low in the sedge community at Island Lake.

Biomass was low for all function groups at both lakes except for the collectors at Island Lake (Table 12). Here the biomass was comparable to the other two communities at the Island Lake when sampled in June and August. This community showed to be productive for the short period it was flooded.

4.5 Temporal Variation of Functional Groups and their Members in Community Plots

Changes in abundance and individual weight for the taxa of functional groups occurred over the sampling season. Abundance and individual weights for the aquatic insects in each community at each lake are presented in the Appendix.

4.5.1 Aquatic Community Plots

Davey Lake was represented by six major taxa and Island Lake by nine. Many taxa increase over the season with numbers and weight per individual being highest later in the season. Dominant taxa over the season at both lakes were the Chironomini (collectors) and Trichocorixa (predators). Tanytarsus (collectors) were also present over the season at Island Lake. Later in the season Ischnura (predators) became quite abundant at Island Lake.

In the aquatic community plot of both lakes, the Chironomini and Trichocorixa were the dominant taxa showing high numbers in June (Table 13). The Chironomini at both lakes increased in abundance and mean individual weight in October. Trichocorixa generally declined through the season in abundance but increased in mean individual weight. Trichocorixa were not collected in July at Davey Lake. Tanyptodinae were present at both lakes through most of the season and in comparatively larger numbers at Davey Lake.

Aquatic communities at both lakes had the largest number of Caenis in October.

The aquatic community at Davey lake was dominated in abundance by predators which is likely due to high numbers of Trichocorixa, where as Island Lake was dominated in abundance by collectors. Island Lake had more taxa and is generally higher in numbers making this aquatic plot more productive in secondary production.

4.5.2 Bulrush Community Plots

The bulrush community at Davey Lake was represented by 11 major taxa while Island Lake had nine taxa (Appendix C). Important taxa over the season at Davey Lake were Caenis and Ischnura whereas at Island Lake the Chironomini and Tanytarsus had greater abundance over the season. Early in the season at Davey Lake, Hydroptila had high numbers and with emergence in May through June. The planktonic early instars were not collected in July possibly due to the mesh size used in sorting. Chironomini were abundant at both plots. Several taxa present in one bulrush plot during certain months were absent in the plot of the other lake. Ischnura was absent in stands at Island Lake in May through July yet were present at Davey Lake at this time. This may have been the result of freezing since Island Lake is shallow. The Chironomini were absent at Davey Lake in May

and June yet were present at Island Lake. When present early in the season, as at Davey Lake, Ischnura's size per individual is relatively large. Much of their weight is gained between the months of October and May.

From the mean weight per individual, it appears that Caenis emerged to adults some time in July as weight per individual decrease from July to August. Mean weight per individual also show that Ischnura grew more rapidly later in the season at Island Lake than at Davey Lake possibly suggesting that prey was more available at Island Lake. Collectors at Davey Lake were also larger in size during most months than those at Island Lake. This implies that greater quantities and/or more nutritious FPOM was present at Davey Lake for these functional groups to utilize.

4.5.3 Sedge Community Plots

Few taxa were represented in the sedge community plots. Four taxa were represented at Island Lake and only one at Davey Lake (Appendix D). All taxa had low numbers except for Tanytarsus at Island Lake where numbers in August were very high. Comparing the mean weight per individual to the other communities during this month, these were relatively small individuals. The sedge plot at Island Lake was flooded for two weeks prior to sampling so the individuals could have been early instars from newly hatched eggs.

Other taxa were collected in these plots (Table 2) but were generally rare and could possibly be associated with adjacent communities, particularly at Island Lake where larger areas encompassing other communities not sampled were flooded by the small rise in lake water level.

CHAPTER 5 CONCLUSION

The hydrologic regime and resulting spatial distribution of surface and ground water in the RLWLA determines the presence and extent of wetland communities. Changes in surface water elevations occurred at both lakes over the season but these changes effected Island Lake more than Davey Lake as a result of the adjacent flatter topography. Though surface elevation changes were relatively small at each lake, rises in surface water flooded more area at Island Lake providing more habitat for aquatic insects, particularly in the sedge communities. This was reflected in the high numbers of Tanytarsus collected in the sedge community after it was flooded for two weeks. The aquatic and bulrush community plots were not noticeably effected by changes in surface water elevations.

The hydrologic gradient differed between the communities of the lakes. Standing water depths in the aquatic community at the Davey Lake sample stands generally were much deeper than those at Island Lake. This had an effect on water temperature and possibly the establishment of aquatic vegetation at Davey Lake as temperatures warmed more slowly in the spring. Little submerged vegetation grew and persisted in the aquatic community at Davey Lake. On

the average the bulrush community sample stands of Davey Lake were 4 cm deeper than those of Island Lake and had a wider range in sampling depths, 43.5 cm compared to 17.6 cm for Island Lake. Temperature and light quality and quantity affecting vegetation could have had an influence on aquatic insect distributions and taxonomic makeup.

Measurements of water pH and conductivity were also studied for their effects on aquatic insect distributions. A conductivity of around 300 $\mu\text{mhos/cm}$ for the two lakes was relatively low compared to that of other wetlands in the northern prairies of North America (LaBaugh 1989). Small changes in conductivity through the sampling period were observed with Davey Lake decreasing and Island Lake increasing. The low conductivity probably was not a factor in determining distributions of aquatic insects. Alkalinity may have played a role limiting the number of species as the waters were around a pH of 9.

Dissolved oxygen had less variation over the day at Davey Lake than Island Lake in September. This may have been due to low production of aquatic vegetation at Davey Lake, depending primarily on diffusion of oxygen from the lake surface. Oxygen levels at Island Lake may have been higher and more stable earlier in the season when vegetation was growing at its peaks. Although early daytime oxygen levels were low in Island Lake, these levels were not

sustained through the day and were determined not to be limiting when compared to other studies of minimal oxygen requirements for aquatic insects.

Differences in organic matter quantity and quality appear to have played a role in aquatic insect distributions. In the bulrush plot at Davey Lake, more coarse particulate organic matter was present. Consequently taxa that require coarse organic material such as Caenis and the caddisflies were more abundant or exclusive to the bulrush plot at Davey Lake.

Vegetation differences were greatest between lakes in the aquatic plots. Davey Lake had very little submerged vegetation where Island Lake supported comparatively more vegetation. Aquatic insects that require vegetation for their habit, such as the Odonata, were lacking in the aquatic community plot at Davey Lake. Abundance and biomass of insects in the aquatic plot at Island Lake were much greater than the similar plot at Davey Lake.

Bulrush community aquatic insect biomass was similar between lakes but abundance and number of taxa was greater at Davey Lake. Vegetation composition was similar at both lakes but bulrush stem density was much greater at Island Lake. Effects from greater stem density such as shading may have played a role in aquatic insect distribution, particularly for the Hydroptila, as it was only found at

Davey Lake in the less dense bulrush plot. Possible relationships to light intensity may be involved with the habitat preference of this caddisfly.

Vegetation and environmental conditions such as organic matter and detritus add substrate complexity to aquatic environments. The least complex environment was the aquatic plot at Davey Lake and the most complex the bulrush plot at Davey Lake. This is reflected in the abundance, biomass, and number of taxa represented by communities. Generally, these two community plots represented the minimum and maximums for these measurements, the bulrush community at Davey Lake having greater values.

Major patterns in the distribution of aquatic insects were seen between the study plots. DCA analysis helped show more clearly which taxa were dominant to the communities plots. A central group of taxa that were common to many of the stands were represented by the Chironomini, Hesperocorixa, Callibaetis and Orthocaldiinae. DCA showed other groupings within community plots such as the caddisflies and Caenis in the bulrush community at Davey Lake which were likely associated with the CPOM found there. The aquatic community of Davey Lake was represented by Trichocorixa. Tanytarsus in the bulrush and sedge communities of Island Lake was associated with more shallow water habitats. Quantitative aspects of vegetation, such as

bulrush stem density, seemed to have an effect on the distribution of Hydroptila, which were more numerous in the less dense stands at Davey Lake.

Time was also a factor in the DCA analysis in the bulrush community of Island Lake. Stand scores through the season progressed by months to their highest values in August then dropped to their lowest values in October. Other communities were not so clear in the progression of stand scores over time.

A factor that was not studied quantitatively, but may have had a significant influence on aquatic insect distribution was that of the presence of carp. Aquatic invertebrates and plant material are taken for food and they may also increase turbidity (Woodling 1985). Several times through the season carp were observed in the bulrush plot of Davey Lake. This could be the reason for the decreases in aquatic insect biomass over the season in the bulrush plot at Davey Lake. The potential for high productivity of aquatic insects in this community was seen from the high biomass produced in May.

Important implications of aquatic insect distributions for waterfowl management can be derived from this data. The importance of vegetation can be seen when comparing productivity of these communities. The sparse vegetation of the aquatic community plot at Davey Lake produced few

aquatic insects, whereas the more heavily vegetated plot at Island Lake was much more productive. Water depth may have played a role in limiting an important potential duck food, the damselfly Ischnura. This species was not present in the earlier part of the season at Island Lake, possibly caused by freezing conditions due to low water levels. If this is the case then raising water levels to protect the Ischnura during the winter could be considered.

Spring use by waterfowl and non-game birds for consumption of aquatic insects would be best at the bulrush community of Davey Lake. At this time Ischnura were near their greatest individual weight. Large numbers of Caenis are also present in the detritus beds in the bulrush and are also relatively large at this time. The adjacent aquatic community at Davey Lake has a large population of Trichocorixa though they have small individual weights at this time.

Through the middle of the season the communities at Davey Lake declined in aquatic insect biomass and Island Lake communities increased. From July through August a major decline in insect biomass is seen in the bulrush community at Davey Lake and Island Lake remains nearly the same. At this time Ischnura emerges into adults contributing to the decline in biomass. Chironomidae numbers and biomass remain at moderate levels in the

communities during this period.

In the fall all communities show a marked increase in abundance and biomass. This is especially true for the bulrush community at Island Lake. Ischnura returns to greater numbers in both communities at Island Lake and in the bulrush community at Davey Lake. Island Lake would be an important waterfowl feeding area during this time as the extent of aquatic vegetation is greater as would be the aquatic insects and other invertebrates.

The importance of the San Luis Valley for supplying ground water for agricultural needs is obvious as seen from the number of center pivot irrigation systems and the numerous artesian wells located in the valley. Recently, efforts have been initiated to further tap the water supplies of the valley for export out of the valley. Lowering the water table could effect the wetlands of the San Luis Valley and in turn alter populations of aquatic insects through loss of habitat. Aquatic and emergent vegetation are key in production of aquatic insects as seen by higher insect biomass and abundance in more vegetated wetland communities at RLWLA. Loss of these wetland through lowering of the water table would effect not only wetland communities and aquatic insects but populations of game and non-game species of birds dependent on these areas for food acquisition and nesting.

5.1 Research Needs

There are few studies addressing the wetlands of the San Luis Valley and I have found no published information on aquatic insects or other invertebrates. One of the primary goals of future research would be to obtain a better understanding of the aquatic insects and their life histories present in the wetlands of the San Luis Valley. Also, characterizing the major wetlands of the area in terms of surface water chemistry, vegetative primary production, and trophic status of major taxa would help to understand and manage this area.

Understanding the role of aquatic vegetation in regulating the abundance of aquatic invertebrates is crucial to the feeding ecology of waterfowl of this area. As previously mentioned in this thesis, many of the lakes in the RLWLA have little established submerged or emergent aquatic flora. Enhancing the growth of aquatic vegetation should, as shown by this study, increase the abundance and biomass of aquatic insects and most likely other aquatic invertebrates having a direct effect on usage by waterfowl and other nongame birds.

The RLWLA and many other areas in the San Luis Valley have large expanses of seasonal wetlands. These wetland types have been shown to be some of the most productive areas in terms of supporting breeding dabbling ducks

(Kantrund and Stewart 1977). The need for high protein food in the spring is essential for the production of waterfowl. Determining the optimal conditions for production of aquatic insect and other invertebrates should be given a priority.

Seasonal wetlands in the San Luis Valley have a diversity of habitats and communities and present an array of different water chemistries able to support many aquatic invertebrate communities. These areas deserve consideration in the overall management of wetland in the Valley.

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APPENDIX A

 Aquatic insect species list for the San Luis Valley, Russell
 Lakes Wildlife Area - 1991

Order	Family	Subfamily	Tribe	Scientific Name	Common Name	Functional Group
Ephemeroptera					Mayflies	
	Baetidae					C
	Caenidae			<u>Callibaetis ferruginea</u> (Walsh)		C
Odonata				<u>Caenis punctata</u> McDunnough	Dragon and damselflies	
	Aeshnidae				Darners	P
	Coenagrionidae			<u>Anax junius</u> Drury	Narrow-winged damselflies	P
Hemiptera				<u>Ischnura perparva</u> Selys	Aquatic bugs	
	Corixidae				Water boatmen	
				<u>Hesperocorixa laevigata</u> (Uhler)		Pi
				<u>Trichocorixa calva</u> (Say)		P
				<u>Sigara alternata</u> (Say)		
Coleoptera					Beetles	
	Gyrinidae			<u>Gyrinus</u> sp.	Whirligig beetles	P
	Haliplidae				Crawling water beetles	P
	Dytiscidae			<u>Halplus</u> sp.	Predaceous diving beetles	P
				<u>Celina</u> sp.		
				<u>Hydroporus</u> sp.		
	Hydrophilidae			<u>Rhantus gutticollis</u> (Say)	Water scavenger beetles	Pi
				<u>Berosus</u> sp.		
	Staphylinidae				Rove beetles	P
	Curculionidae				Weevils	S
Trichoptera					Caddisflies	
	Hydroptilidae				Micro caddisflies	Pi
				<u>Hydroptila ajax</u> Ross		
	Phryganeidae					S
	Leptoceridae			<u>Phryganea cinerea</u> Walker	Longhorned case makers	
				<u>Mystacides interjecta</u> (Banks)		C
				<u>Oecetis</u> sp.		P
				<u>Triaenodes</u> sp.		S
Diptera					Crane flies	S
	Tipulidae				Mosquitoes	C
	Culicidae			<u>Anopheles</u> sp.	Biting midges	P
	Ceratopogonidae			<u>Culicoides</u> sp.	Non-biting midges	
	Chironomidae					
		Tanypodinae		<u>Larsia</u> sp.		P
				<u>Procladius</u> sp.		
		Orthoclaadiinae				
			Orthoclaadiini	<u>Cricotopus</u> sp.		S
		Chironominae				
			Chironomini	<u>Chironomus</u> sp.		C
				<u>Cryptochironomus</u> sp.		
				<u>Dicrotendipes</u> sp.		
			Tanytarsini	<u>Tanytarsus</u> sp.		

(continued)

APPENDIX A (continued)

Order	Family	Subfamily Tribe	Common Name	Functional Group
	Dixidae		Dixid midges	C
	Tabanidae	<u>Dixa</u> sp.	Horse and deer flies	P
		<u>Chrysops</u> sp.		
	Dolichopodidae		Shore flies	C
	Ephydriidae		Dung flies	S
	Scathophagidae			

C = collector P = predator S = shredder Pi = piercer herbivore

APPENDIX B

Monthly mean abundance and mean weight per individual per m² for dominant taxa of functional groups represented in the aquatic community plots at Davey and Island Lakes, Saguache County, Colorado, 1991. N.S. = not sampled, mg / ind. = mg/individual.

Lake	29 May		15 June		19 July		23 August		18 September		21 October	
Functional group Taxa	mean abund.	(mg/ ind.)	mean abund.	(mg/ ind.)	mean abund.	(mg/ ind.)	mean abund.	(mg/ ind.)	mean abund.	(mg/ ind.)	mean abund.	(mg/ ind.)
Davey Lake												
Collectors												
Chironomini*	N.S.		125	(0.10)	36	(0.10)	47	(0.10)	21	(0.10)	79	(0.21)
Tanytarsus			0	0	0	0	0	0	0	0	14	(0.05)
Caenis			18	(0.40)	0	0	0	0	0	0	29	(0.15)
Callibaetis			0	0	0	0	0	0	0	0	0	0
Predators												
Tanypodinae**			4	(0.45)	36	(0.17)	11	(0.20)	0	0	32	(0.13)
Trichocorixa			370	(0.05)	0	0	83	(0.16)	32	(0.26)	11	(0.35)
Ischnura			0	0	0	0	0	0	0	0	0	0
Anax			0	0	0	0	0	0	0	0	0	0
Piercers												
Hesperocorixa***			0	0	0	0	4	(0.63)	0	0	0	0
Hydroptila			0	0	0	0	0	0	0	0	0	0
Shredders												
Phryganea			0	0	0	0	0	0	0	0	0	0
Island Lake												
Collectors												
Chironomini*	194	(0.08)	456	(0.10)	327	(0.10)	147	(0.11)	208	(0.10)	391	(0.16)
Tanytarsus	4	(0.11)	36	(0.09)	25	(0.19)	43	(0.12)	18	(0.18)	18	(0.12)
Caenis	0	0	4	(0.11)	0	0	4	(0.11)	35	(0.07)	36	(0.17)
Callibaetis	0	0	0	0	0	0	18	(2.24)	18	(0.14)	32	(0.36)
Predators												
Tanypodinae**	0	0	4	(0.11)	18	(0.32)	25	(0.29)	7	(0.31)	108	(0.12)
Trichocorixa	4	(0.19)	140	(0.09)	166	(0.53)	79	(0.68)	43	(0.58)	47	(0.45)
Ischnura	0	0	0	0	0	0	22	(0.78)	126	(0.86)	118	(1.13)
Anax	0	0	0	0	0	0	0	0	4	(4.30)	0	0
Piercers												
Hesperocorixa***	0	0	0	0	14	(0.60)	36	(0.78)	29	(2.70)	7	(2.00)
Hydroptila	0	0	0	0	0	0	0	0	0	0	0	0
Shredders												
Phryganea	0	0	0	0	0	0	0	0	0	0	0	0

* Includes Chironomus, Dicrotendipes, and Cryptochironomus

** Includes Larsia and Procladius.

*** Includes Sigara.

APPENDIX C

Monthly mean abundance and mean weight per individual per m² for dominant taxa of functional groups represented in the bulrush community plots at Davey and Island Lakes, Saguache County, Colorado, 1991. N.S. = not sampled, mg/ind. = mg/individual.

Lake Functional group Taxa ind.)	29 May		15 June		19 July		23 August		18 September		21 October	
	mean abund.	(mg/ ind.)	mean abund.	(mg/ ind.)	mean abund.	(mg/ ind.)	mean abund.	(mg/ ind.)	mean abund.	(mg/ ind.)	mean abund.	(mg/ ind.)
Davey Lake												
Collectors												
Chironomini*	0	0	0	0	104	(0.21)	284	(0.16)	58	(0.23)	237	(0.17)
Tanytarsus	14	(0.10)	7	(0.10)	7	(0.31)	25	(0.10)	7	(0.16)	54	(0.07)
Caenis	649	(0.19)	423	(0.20)	355	(0.42)	136	(0.19)	251	(0.09)	492	(0.14)
Callibaetis	0	0	0	0	4	(1.63)	18	(1.77)	0	0	0	0
Predators												
Tanypodinae**	0	0	0	0	4	(0.10)	4	(0.10)	14	(0.31)	7	(0.35)
Trichocorixa	0	0	0	0	4	(0.45)	50	(0.29)	0	0	0	0
Ischnura	61	(2.64)	36	(2.60)	22	(6.11)	25	(0.23)	29	(0.39)	61	(0.51)
Anax	0	0	0	0	4	(0.10)	11	(0.26)	0	0	0	0
Piercers												
Hesperocorixa***	0	0	0	0	0	0	0	0	18	(3.55)	0	0
Hydroptila	452	(0.38)	7	(0.26)	0	0	108	(0.19)	0	0	0	0
Shredders												
Phryganea	0	0	0	0	0	0	7	(1.03)	0	0	4	(15.70)
Island Lake												
Collectors												
Chironomini*	29	(0.13)	54	(0.07)	65	(0.09)	258	(0.08)	239	(0.13)	503	(0.21)
Tanytarsus	57	(0.09)	413	(0.06)	1285	(0.05)	337	(0.08)	59	(0.09)	32	(0.08)
Caenis	4	(0.19)	0	0	0	0	4	(0.11)	0	0	4	(0.19)
Callibaetis	0	0	0	0	0	0	4	(1.31)	0	0	7	(0.44)
Predators												
Tanypodinae**	0	0	0	0	11	(0.27)	47	(0.19)	25	(0.26)	40	(0.34)
Trichocorixa	0	0	0	0	0	0	0	0	0	0	0	0
Ischnura	0	0	0	0	0	0	43	(0.26)	65	(0.94)	179	(0.82)
Anax	0	0	0	0	4	(10.47)	11	(2.76)	7	(4.90)	14	(15.77)
Piercers												
Hesperocorixa***	0	0	0	0	4	(0.69)	0	0	0	0	0	0
Hydroptila	0	0	0	0	0	0	0	0	0	0	0	0
Shredders												
Phryganea	0	0	0	0	0	0	0	0	0	0	0	0

* Includes Chironomus, Dicrotendipes, and Cryptochironomus

** Includes Larsia and Procladius.

*** Includes Sigara.

APPENDIX D

Monthly mean abundance and mean weight per individual per m² for dominant taxa of functional groups represented in the sedge community plots at Davey and Island Lakes, Saguache County, Colorado, 1991. N.S. = not sampled, mg/ind. = mg/individual.

Lake Functional group Taxa	29 May		15 June		19 July		23 August		18 September		21 October	
	mean abund.	(mg/ ind.)	mean abund.	(mg/ ind.)	mean abund.	(mg/ ind.)	mean abund.	(mg/ ind.)	mean abund.	(mg/ ind.)	mean abund.	(mg/ ind.)
Davey Lake												
Collectors												
Chironomini*	N.S.		N.S.		N.S.		N.S.		4	(0.09)		N.S.
Tanytarsus									0	0		
Caenis									0	0		
Callibaetis									0	0		
Predators												
Tanypodinae**									0	0		
Trichocorixa									0	0		
Ischnura									0	0		
Anax									0	0		
Piercers												
Hesperocorixa***									0	0		
Hydroptila									0	0		
Shredders												
Phraganea									0	0		
Island Lake												
Collectors												
Chironomini	N.S.		4	(0.30)	N.S.		4	(0.10)		N.S.		N.S.
Tanytarsus			0	0			857	(0.07)				
Caenis			0	0			4	(0.11)				
Callibaetis			0	0			0	0				
Predators												
Tanypodinae*			0	0			0	0				
Trichocorixa			0	0			0	0				
Ischnura			0	0			4	(0.19)				
Anax			0	0			0	0				
Piercers												
Hesperocorixa**			1	(0.89)			0	0				
Hydroptila			0	0			0	0				
Shredders												
Phryganea			0	0			0	0				

* Includes Chironomus, Dicrotendipes, and Cryptochironomus

** Includes Larsia and Procladius.

*** Includes Sigara.