AQUATIC MACROINVERTEBRATE LIFE HISTORY AND PHENOLOGY IN A COLORADO ALPINE WETLAND (GREEN LAKES VALLEY, COLORADO FRONT RANGE)

By

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AQUATIC MACROINVERTEBRATE LIFE HISTORY
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WETLAND (GREEN LAKES VALLEY,
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CHAPTER I

INTRODUCTION

Alpine Aquatic Insects

Important limiting characteristics to aquatic insects in the arctic/alpine environment are low temperature, low annual heat budgets, and severe and variable weather (Downes 1964). Alpine is defined as the high elevation region above the krumholtz. Temperate macroinvertebrate assemblages have been extensively studied (Anderson and Cummins 1979, Coffman 1971, Cummins 1979, Merrit and Cummins 1984). Alpine macroinvertebrate assemblages have received little attention primarily due to inaccessibility of study sites. Studies have been conducted in Alaska and Colorado dealing with life cycles, feeding strategies, and distribution of arctic and montane macroinvertebrates (Butler 1980, Gray and Ward 1979, Martinson and Ward 1982). Little is known about alpine macroinvertebrate life histories or the factors influencing their distribution and abundance.

Colorado alpine lakes and streams have recieved little study. High altitude (>3000 m) stream studies are far fewer in number than lake studies (Bushnell et. al.

1986). Elgmork and Saether (1970) and Saether (1970) performed an alpine stream study in the Green Lakes Valley of the Colorado Front Range. Other studies above 3000 m are those of Dodds and Hisaw (1925), Short and Ward (1980), and Ward (1986). The Green Lakes Valley study (Elgmork & Saether 1970, Saether 1970) is most germaine to the present work and was performed in the same valley.

Arctic studies are somewhat related to alpine studies due to similar temperature regimes. Arctic studies indicate that the seasonal timing of life cycle events and population age structure are closely related to temperature and heat budgets (Oliver 1968, Butler 1982). Alpine aquatic macroinvertebrates have recieved little attention but are believed to exhibit similar seasonal timing and to have a similar age structure as arctic species.

Chironomidae tend to dominate alpine aquatic environments as they do in the arctic (Oliver 1968, Elgmork & Saether 1970). Arctic studies have described multi-year life cycle strategies, usually coupled with a single emergence period per year, in chironomidae (Oliver 1968, Butler 1982, Pinder 1986). A multi-year life cycle in the alpine or arctic is believed to be an adaptation to temperature (Danks 1964, Oliver 1968, Downes 1971, Butler 1982). Studies of arctic chironomidae show that the emergence period is associated with an increase in temperature and occurs before water reaches maximum temperature (Oliver 1968, Boeger 1981). Danks and Oliver (1972) describe the synchrony of emergence in 11 chironomid species within arctic ponds. They showed that time of emergence can be prolonged by low temperatures. The threshold for emergence is about 7 degrees Celcius. They also found a temperature requirement of 4 - 5 degrees Celcius for pre-emergence development to occur.

Trichoptera have recieved little attention in the alpine. They are generally known to be univoltine (Anderson & Wold 1972, Canton & Ward 1981, Martinson & Ward 1982). However, Iverson (1976) described a 2 year life cycle for Parachiona Picornis in a cold-water Danish spring. Most mountain caddisflies are detritus shredders which emerge in mid to late summer and develop through five instars (Canton & Ward 1981).

The purpose of this study was to describe the species composition, dominant insect age distribution, food habits and insect emergence phenology of a Colorado alpine wetland.

CHAPTER II

STUDY SITE

The wetland study site is located in the Green Lakes Valley of the Colorado Front Range (Figure 1). The valley is within the City of Boulder Watershed where human access and activity is restricted. One entry road allows vehicle access only as far as Green lake 1 (elevation 3400 m). Two weather stations are located in the valley, one at the Arikaree glacier and one near Green Lake 4 (Figure 1).

The 2 ha wetland is located in the upper Green Lakes Valley at an elevation of 3600 m between Green Lakes 4 and 5. Dominant plants in the wetland are sedge (<u>Carex</u>) and willow (<u>Salix</u>). Five study pools are identified in the wetland (Figure 2). Water input to the wetland is primarily from the rock glacier (snowfield). Discharges are highest during early summer (personal observation). A temperature gradient exists from the inlet to the outlet in the wetland. Generally, the inlet is 2-3 degrees Celcius colder than the outlet throughout the summer (unpublished LTER data). The pools vary in water surface area and depth with the shallow, high surface area pool (A) nearest the inlet. Data on the volume,

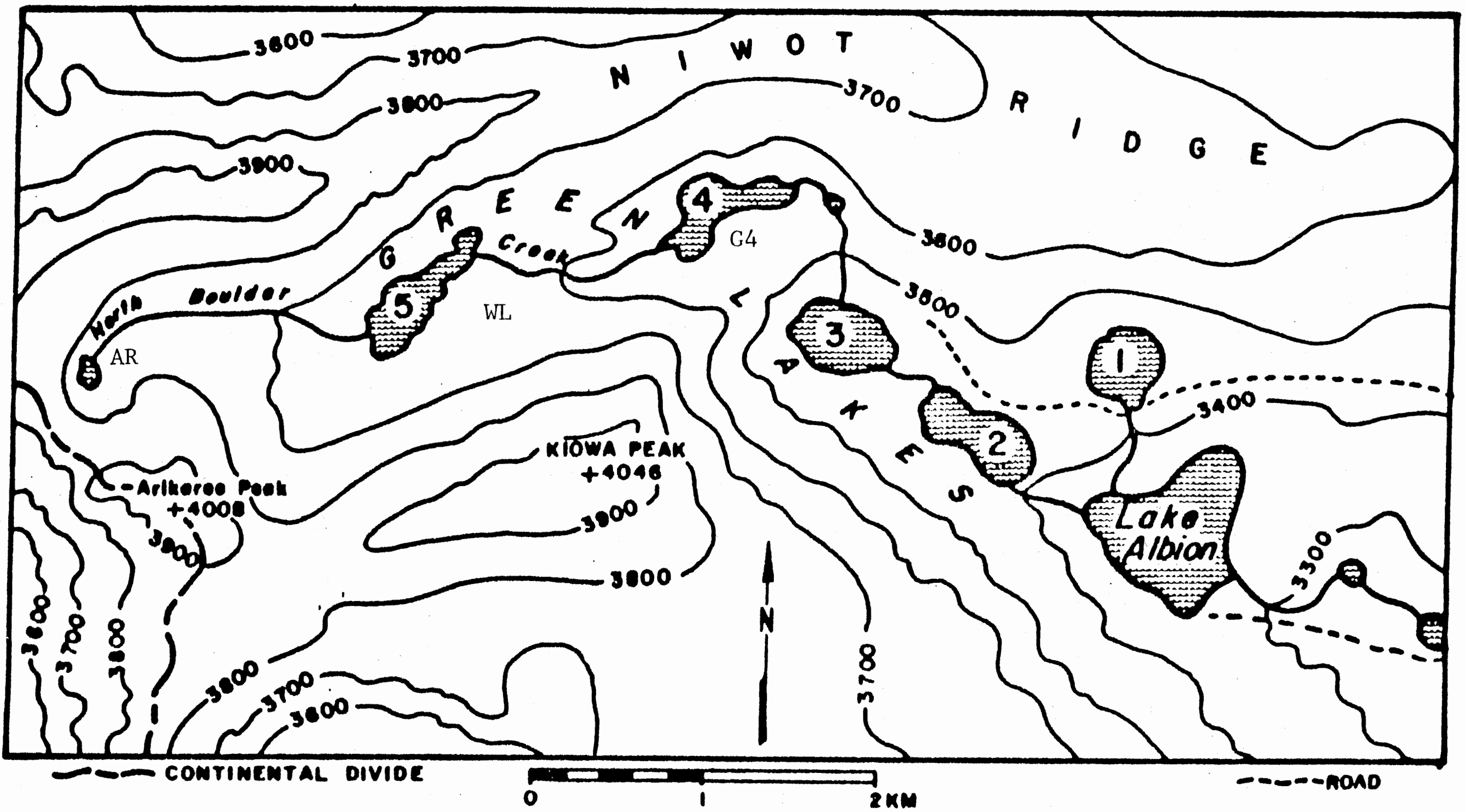

Figure 1. Location Map of the Green Lakes Valley.
WL = Wetland
AR = Arikaree Weather Station
G4 = Green Lake 4 Weather Station.

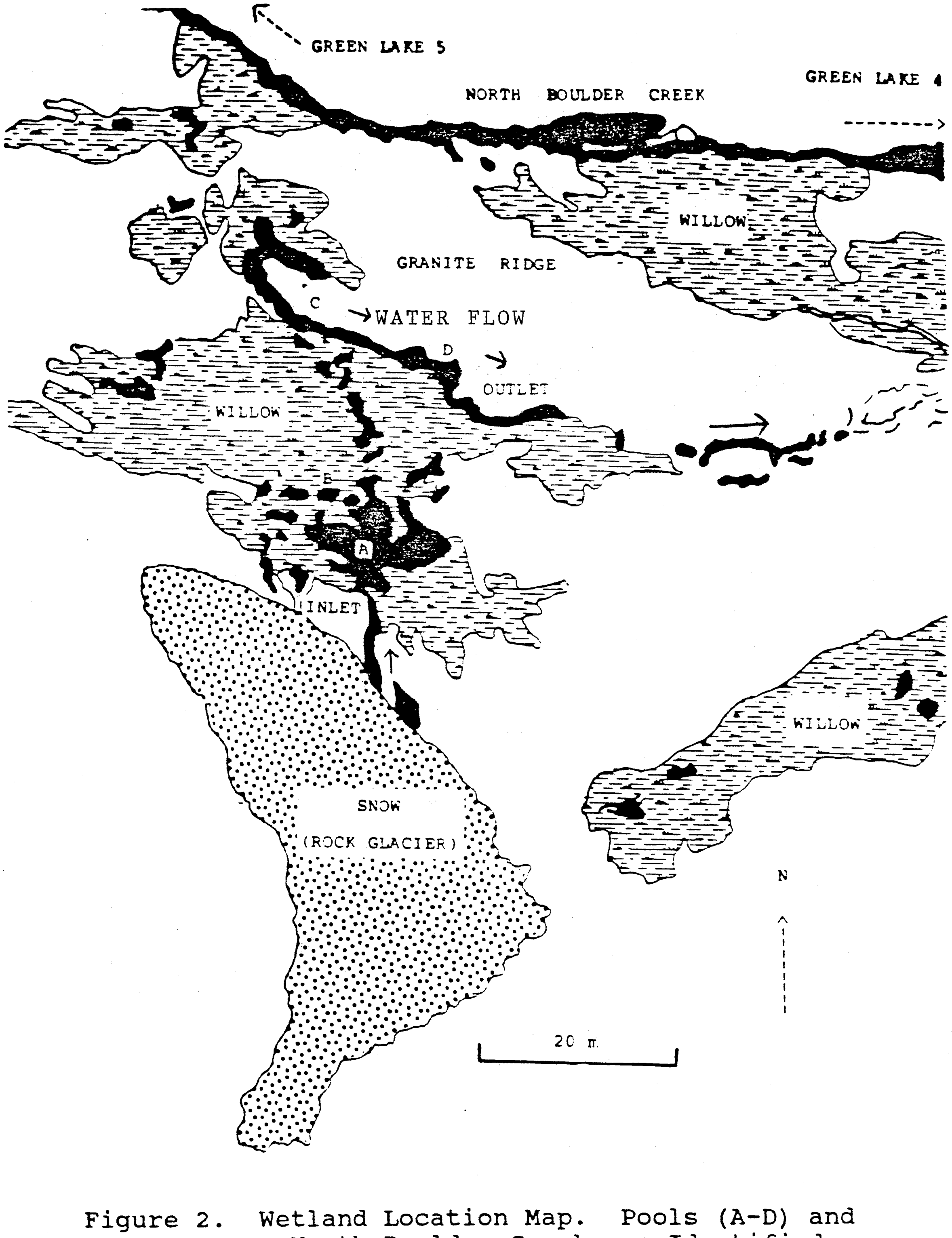

Figure 2. Wetland Location Map. Pools (A-D) and North Boulder Creek are Identified in Black.

area and flow in the various pools are unavailable, but they are less than 1 - 2m wide. The wetland pools have a maximum depth of 0.5 to 1 m. Pools A and B have primarily sediment substrate. Pools C, D, and outlet have primarily rock substrate.

CHAPTER III

METHODS

Physical Factors

Temperature was monitored hourly with two Ryan Tempmentor recording thermographs at the sediment surface and at 10 cm depth in the outlet pool between June and October during 1987 and 1988. Daily average temperature data for 1987 and 1988 were obtained from the Arikaree glacier weather and the Green Lake 4 weather stations. Mark Loseleben, climatologist at the University of Colorado Mountain Research Station, provided the data from the weather stations.

Species Composition of Aquatic Insects

Identification of taxa was made using keys in Wiggins (1977), Oliver (1981), Cranston et. al. (1983) and Merritt & Cummins (1984). The lowest possible level of identification was made for all organisms.

The species composition of the aquatic invertebrates in the wetland was determined by sampling the aquatic fauna with drift nets (363 micron mesh) placed at the inlet and outlet of the wetland from July 1 to August 14, 1986 and June 10 to October 1 during 1987 and 1988. Each net had a 25cm x 48cm rectangular opening. In 1986 the outlet net was baffled on both sides with plywood to channel all water flow through the net. No baffles were used with the outlet drift net in 1987 and 1988. The inlet drift net was placed directly at the inlet and needed no modification to filter all flow in the channel. The nets were emptied of all material weekly and samples preserved in 95% ETOH. Emergence traps, and artificial substrate samplers (both described below) were also used.

Aquatic Insect Spatial and Temporal Distribution

Multiplate artificial substrate samplers (Hester & Dendy 1962) were used for determining dipteran age distribution and food habits in 1987 and 1988. Each sampler contained 14 square particle board plates (7.6 cm x 7.6 cm) mounted on an eye bolt. Two small plates (2.6 cm x 2.6 cm) were placed on the eye bolt between each of the larger plates to allow 1 cm of space between them. The sampling design appears in Table 1.

TABLE 1

MULTIPLATE ARTIFICIAL SUBSTRATE SAMPLING DESIGN

SAMPLE	NUMBER OF SAMPLES PER SITE			
	1987		1988	
	AUG 24	SEP 16	AUG 18	SEP 12
OUTLET	2	2	5	5
POOL D	1	2	4	3
POOL B	2		3	2
POOL A			4	

During 1987 and 1988, respectively, each sampler was placed at least 2 months prior to removal. After removal from the wetland, each sampler was placed in a 1 l plastic bag (Ziploc) and transported to the laboratory. There it was disassembled and the plates were scraped with a razor blade to remove all organisms and tube cases.

Core samples for Diptera were taken in 1987 with a Wildco brass core sampler (model 2424 A15). The sediment was cored to a depth of 10 cm with a 5 cm diameter core tube. Ten samples were taken in the outlet pool on June 2, 1987 and five samples in pool D on June 8, 1987.

Quadrat samples were used for determining trichopteran age distribution and food habits during the summer of 1987 and 1988. The method involved placing a wire square (10 cm^2) on the substrate at random. Then all animals were removed with forceps from the substrate within the grid. This method was used on rock substrate and sediment substrate in the outlet pool once a week during the summer of 1987 and 1988, (n=5), respectively.

All samples were preserved in 95% ETOH. Substrate and core samples were sorted for organisms using the sucrose flotation method (Anderson 1959). The head capsule width of each larvae was measured to the nearest 0.02mm with a Reichert stage micrometer and 10-90x Bausch & Lomb dissecting stereo-microscope.

Aquatic Insect Emergence

Aquatic insect emergence was monitored in 1987 and 1988 using floating circular emergence traps. Each funnel covered 0.1 m^2 of water surface and was constructed of flexible clear plastic molded into a cone. A killing jar was located at the top of the cone where emerging insects were retained and killed with a formalin-soaked sponge. The plastic cone was anchored to a square floating wood platform. The bottom of the cone was kept at least 5 cm under the water surface. Each floating platform was anchored to a stainless steel pole which had been driven into the sediment. Three traps were placed in the outlet pool and two in pool D on June 10, 1987 and removed on September 30, 1987. Traps were emptied every 3 to 4 days in 1987, but results appear on a weekly basis. Four traps were placed in the outlet pool and three in pool D on June 8, 1988 and removed on September 30, 1988. During 1988 traps were emptied weekly. Samples were preserved in 95% ETOH and identified using a 10-90x Bausch & Lomb dissecting stereo-microscope.

Aquatic Insect Food Habits

Five insects of each instar of <u>Asynarchus</u> were examined for gut contents. The mid and foregut of each insect was removed by dissection at 10x and prepared as in Coffman (1971). The stomach contents were separated from the intestine wall with a scalpel. The stomach contents were then diluted with 25 ml distilled water. This mixture was shaken for 30 sec and then filtered through a gridded 0.45 u Millipore filter. The filter was cleared with immersion oil for 24 h and then mounted with Euparol on a slide for later inspection with a Nikon binocular microscope at 400 x. The categories of food were:

1. Filamentous algae
2. Unrecognizable detritus
3. Diatoms
4. Other

The food composition (% occurrence by weight) of each gut was determined for these categories. The total number of algal cells and diatom frustules per one grid area of each filter was determined. This number was then converted to weight per grid area using 8.34 x 10^{-6} mg as a mean weight per cell or frustule (Coffman 1971). The total area of each detrital particle (recorded by maximum diameter) was determined. Then the total area of detrital particles per one grid area on each filter was determined. This detrital area per grid was then converted to weight per grid area using 0.0303 mg/mm^2 (Coffman 1971).

Dipteran gut contents were analyzed for the presence or absence of each food category. At least two individuals of each species were inspected using a slide mount of the foregut contents. All inspections were made at 400 x with a Nikon binocular microscope.

CHAPTER IV

RESULTS

Physical Factors

Wetland sediment temperature, daily average air temperature at the Arikaree weather station, and daily average air temperature at the Green Lake 4 weather station for 1987 and 1988 appear in Appendices A-C. Since wetland temperature monitoring began in June during both years, there are no direct measurements for April and May. However, an estimate of those temperatures was made as follows. Wetland sediment daily average temperature (10cm depth) for April, May, and early June of 1987 was back-calculated using the relationship between the wetland sediment temperature and air temperature at the Arikaree weather station. Between June 28 and July 5 there was a linear relationship between the variables ($r = 0.76$). The following equation was used to predict sediment temperatures: $y = 0.4x + 1.96$, where y is the wetland sediment temperature and x is Arikaree air temperature. In a similar way, wetland sediment daily average temperature at 10cm depth for April and May of 1988 was back-calculated from a regression of June 10-15 data between the wetland sediment and the Arikaree weather station (r= 0.99). The equation was as follows: $y = 0.23\ x + 1.58$, where y is wetland sediment temperature and x is Arikaree air temperature.

Data from all temperature recording sites (Wetland, Arikaree and Green lake 4) for 1987 and 1988 are summarized as cumulative degree days per month to indicate seasonal trends in climate (Figure 3). The data are tabulated in Appendix D. Most of the accumulation of degree days occurred during July, August and September. Total cumulative degree days by month for the growing season at each temperature recording site in 1987 and 1988 appears in Figure 4. During 1987 there was an early spring warming trend which did not occur in 1988, resulting in higher degree day accumulation early in 1987 (Figures 3 and 4). For example, in April 1987 the cumulative degree days were 33.5, 7.7, and 41.7 for Green Lake 4, Arikaree, and the wetland sediment, respectively (Appendix D). In 1988 the cumulative degree days for April were 11.7, 2.0, and 13.9, for Green Lake 4, Arikaree, and the Wetland sediment, respectively (Appendix D). Thus, 1987 exhibited nearly three times the heat accumulation than 1988 at all three temperature monitoring sites during the spring.

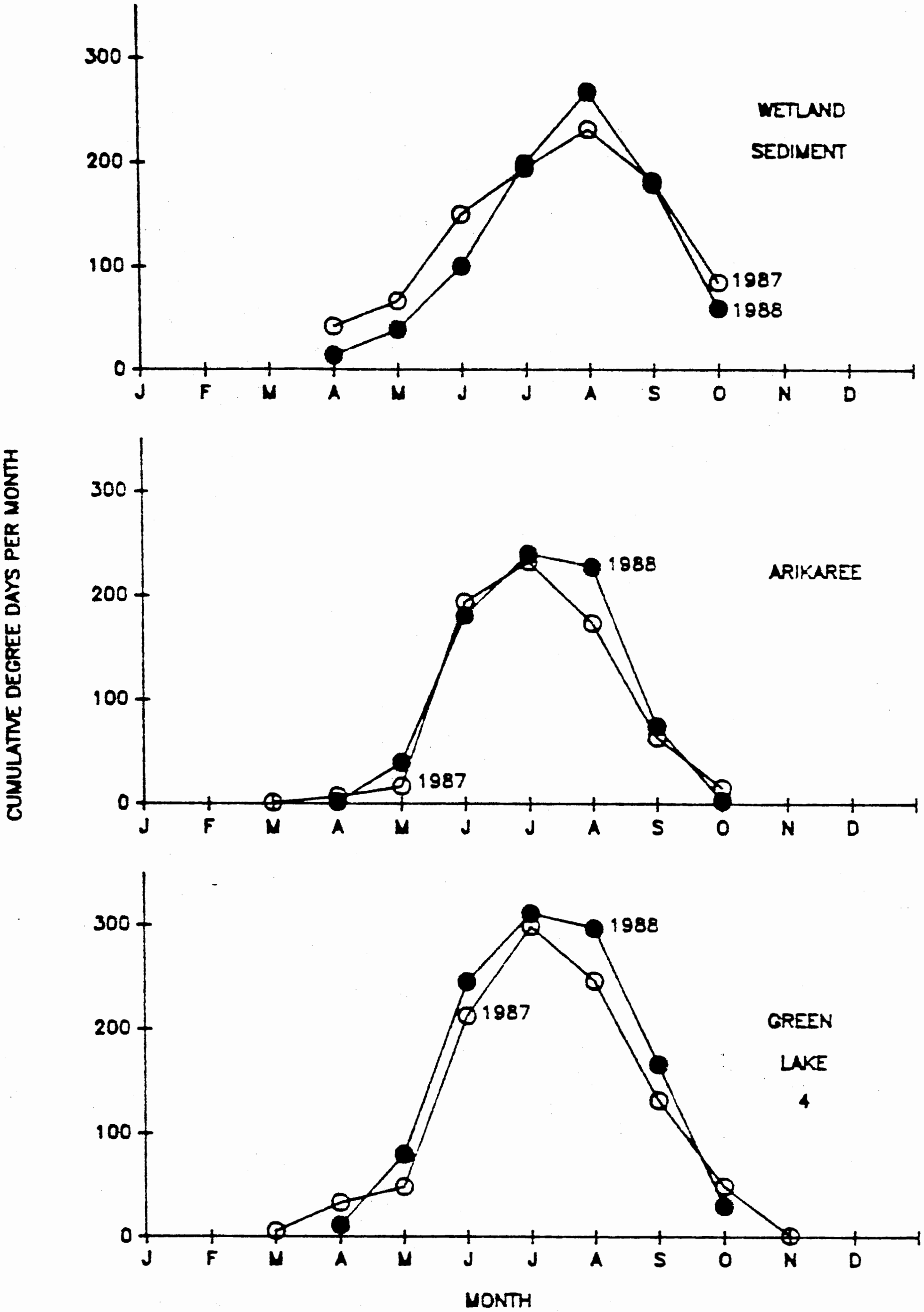

Figure 3. Cumulative Degree Days per Month for 1987 and 1988 in the Wetland Sediment (10 cm depth), at the Arikaree Weather Station and at the Green Lake 4 Weather Station.

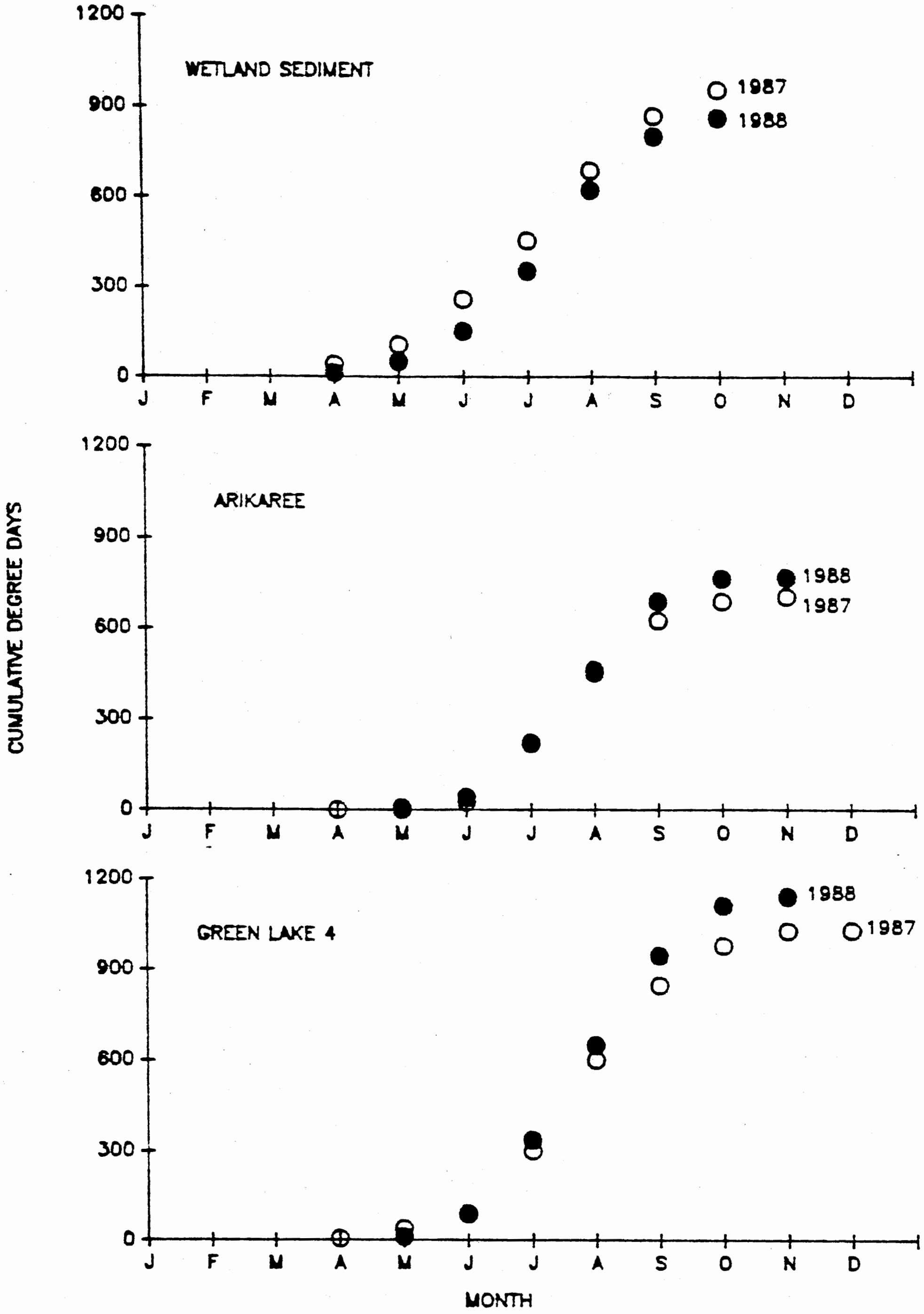

Figure 4. Total Cumulative Degree Days by Month for 1987 and 1988 in the Wetland Sediment (10 cm depth), at the Arikaree Weather Station and at the Green Lake 4 Weather Station.

Degree day accumulation by month was slightly higher during the summer of 1988 than 1987 (Figure 3). After June the total cumulative degree days was higher during 1988 than during 1987 at Arikaree and Green Lake 4 although not in the wetland sediment (Figure 4). Thus, by the end of the summer, there were more cumulative degree days in 1988 as measured by air temperatures, but less cumulative degree days in 1988 as measured by sediment temperatures (Figure 4).

Species Composition of Aquatic Insects

The eight aquatic insect taxa collected in 1986 were dominated by two dipteran genera (*Orthocladius* spp. and *Pseudodiamesia* sp.) and one trichopteran (*Asynarchus* sp.) (Table 2). *Orthocladius* spp. represents two different species (Dr. William Coffman, Pers. Comm.). Hymenoptera, family Diapriidae, was found in relatively small numbers, while the other taxa occurred infrequently in 1986. One dipteran (*Orthocladius* spp.), and one trichopteran (*Asynarchus* sp.) dominated the 20 taxa collected each year in 1987 and 1988 (Table 2).

TABLE 2

TAXA COLLECTED FROM DRIFT INLET (I) AND OUTLET (O), SUBSTRATE (S), AND EMERGENCE (E) SAMPLES IN 1986, 1987, AND 1988 IN A COLORADO ALPINE WETLAND

	7/1-8/14/86			6/1-10/30/87				6/1-10/30/88			
ORGANISM	I	O	E	I	O	S	E	I	O	S	E
Coleoptera											
Carabidae				*				*			
Elmidae	*										
Haliplidae				*				*			
Dytiscidae											
Agabus sp.							*				*
Collembola											
Isotomidae											
Isotomus sp.	*			*				*			
Diptera											
Anthericidae							*				*
Blephariceridae							*				*
Chironomidae											
Diamesia sp.						*	*				*
Microspectra sp.						*				*	
Orthocladius spp.		*	*	*	*	*	*		*	*	*
Phaenospectra sp.					*	*			*	*	*
Pseudodiamesia sp.		*	*			*				*	
Trichotanypus sp.						*	*			*	*
Ephyridae			*								
Sciomyzidae							*				*
Simuliidae							*				*
Homoptera											
Cicadellidae				*				*			
Veliidae											
Microvelia sp.			*								
Hymenoptera											
Braconidae							*				*
Diapriidae							*				*
Plecoptera											
Nemouridae							*				*
Trichoptera											
Limnephilidae											
Asynarchus sp.		*	*		*		*		*		*
Ostracoda											
Cyprididae											
Cypricercus sp.				*	*			*	*		

* indicates presence of the taxa in any sample during the sampling period.

Aquatic Insect Spatial and Temporal Distribution

No organisms were collected in any core sample in 1987. Chironomid distribution from substrate sampling in the wetland during 1987 and 1988 is summarized in Table 3. A more complete list appears in Appendices E and F. During both years the dominant chironomid was Orthocladius spp. which declined in abundance between August and mid-September. All other taxa were present in such small numbers that temporal or spatial distribution trends were undetectable. Based on head capsule measurements, only one size class was found for all species during both years indicating univoltinism in all diptera (Table 4).

Diversity indices were calculated from a computer program written in BASIC (Brower & Zar 1984). Five species diversity indices are compared for each sample date and site (Table 5). Two species richness indices and three dominance indices were used for comparison. In 1987, the outlet pool had the highest diversity of all sites within the wetland. High diversity was found in the outlet pool in 1988. Pools A and B had high diversity in August 1988.

TABLE 3

AVERAGE NUMBER OF CHIRONMIDAE COLLECTED PER SUBSTRATE SAMPLER IN THE OUTLET AND POOLS IN A COLORADO ALPINE WETLAND

Sample date(site)	OR	MS	PH	PS	TR
8-24-87					
(outlet)	61.3	9.3	2.3	0.7	
(pool D)	48.0	9.0		2.0	
(pool B)	62.5		0.5		
9-16-87					
(outlet)	8.5	4.5	1.0	1.5	
(pool D)	14.5	3.0		0.5	
(pool B)	161.5	2.0	10.0		
8-18-88					
(outlet)	32.0	3.2	7.8	3.6	0.8
(pool D)	24.0	0.7	14.3	0.8	
(pool B)	33.7	14.3	15.3	6.7	
(pool A)	33.0	12.8	14.0	15.5	
9-12-88					
(outlet)	10.0	6.8	7.0	0.8	0.4
(pool D)	13.5	0.8	9.3	0.5	
(pool B)	67.5	7.0	52.5	0.5	

OR = _Orthocladius_ spp.
MS = _Microspectra_ sp.
PH = _Phaenospectra_ sp.
PS = _Pseudodiamesia_ sp.
TR = _Trichotanypus_ sp.

TABLE 4

HEAD CAPSULE WIDTH OF CHIRONOMID SIZE CLASSES FROM SUBSTRATE SAMPLES

YEAR SAMPLED	HEAD CAPSULE WIDTH (mm)				
	OR	MS	PH	PS	TR
1987	0.3	0.5	0.3	0.6	0.4
1988	0.2	0.5	0.3	0.6	0.4

OR = *Orthocladius* spp.
MS = *Microspectra* sp.
PH = *Phaenospectra* sp.
PS = *Pseudodiamesia* sp.
TR = *Trichotanypus* sp.

TABLE 5

SPECIES DIVERSITY OF BENTHIC MACROINVERTEBRATES IN THE SUBSTRATE OF A COLORADO ALPINE WETLAND

Sample date (site)	DIVERSITY INDEX				
	Species Richness		Dominance		
	Margalef	Mehinick	Brillouin	Simpson	Shannon
8-24-87					
(outlet	1.61	0.47	0.22	0.29	0.25
(pool D)	1.12	0.39	0.22	0.32	0.20
(pool B)	0.55	0.25	0.03	0.02	0.02
9-16-87					
(outlet)	2.52	1.00	0.40	0.64	0.47
(pool D)	1.59	0.71	0.23	0.34	0.25
9-30-87					
(pool B)	0.89	0.22	0.11	0.13	0.12
8-18-88					
(outlet)	2.38	0.73	0.40	0.52	0.44
(pool D)	1.80	0.63	0.23	0.52	0.36
(pool B)	1.62	0.48	0.53	0.68	0.50
(pool A)	1.60	0.46	0.54	0.71	0.56
9-12-88					
(outlet)	2.86	1.00	0.43	0.71	0.54
(pool D)	2.17	0.81	0.35	0.56	0.38
(pool B)	1.42	0.35	0.37	0.45	0.38

Index calculations are found in Brillouin (1962), Margalef (1968), Menhinick (1976), Shannon (1948), and Simpson (1949).

The instar stages of Asynarchus sp. were determined by head capsule width (Figure 5). The temporal distribution of Asynarchus for 1987 and 1988 appears in Figures 6 and 7. During 1987 Asynarchus sp. was present as instar IV 2 wk earlier than in 1988. This later calendar date for the same life cycle event in 1988 appears in every Asynarchus sp. life stage (Figures 6 and 7) and is always 2 to 3 wk later in 1988. In 1987 Asynarchus sp. pupated by July 12 while in 1988 it did not pupate until July 26.

The distribution of Asynarchus sp. on rock and sediment substrate types in 1987 and 1988 is shown in Figure 8. During 1987, most instar IV larvae were collected on rock substrate while instar V and pupae were found on sediment substrate. Asynarchus sp. instar III, IV and V larvae did not appear to have a substrate preference in 1988. Pupae prefered rock substrate for development in 1988. Just prior to pupation during both years larvae were noted to build a case of small stones (<1mm) around a pre-existing case built of leaves.

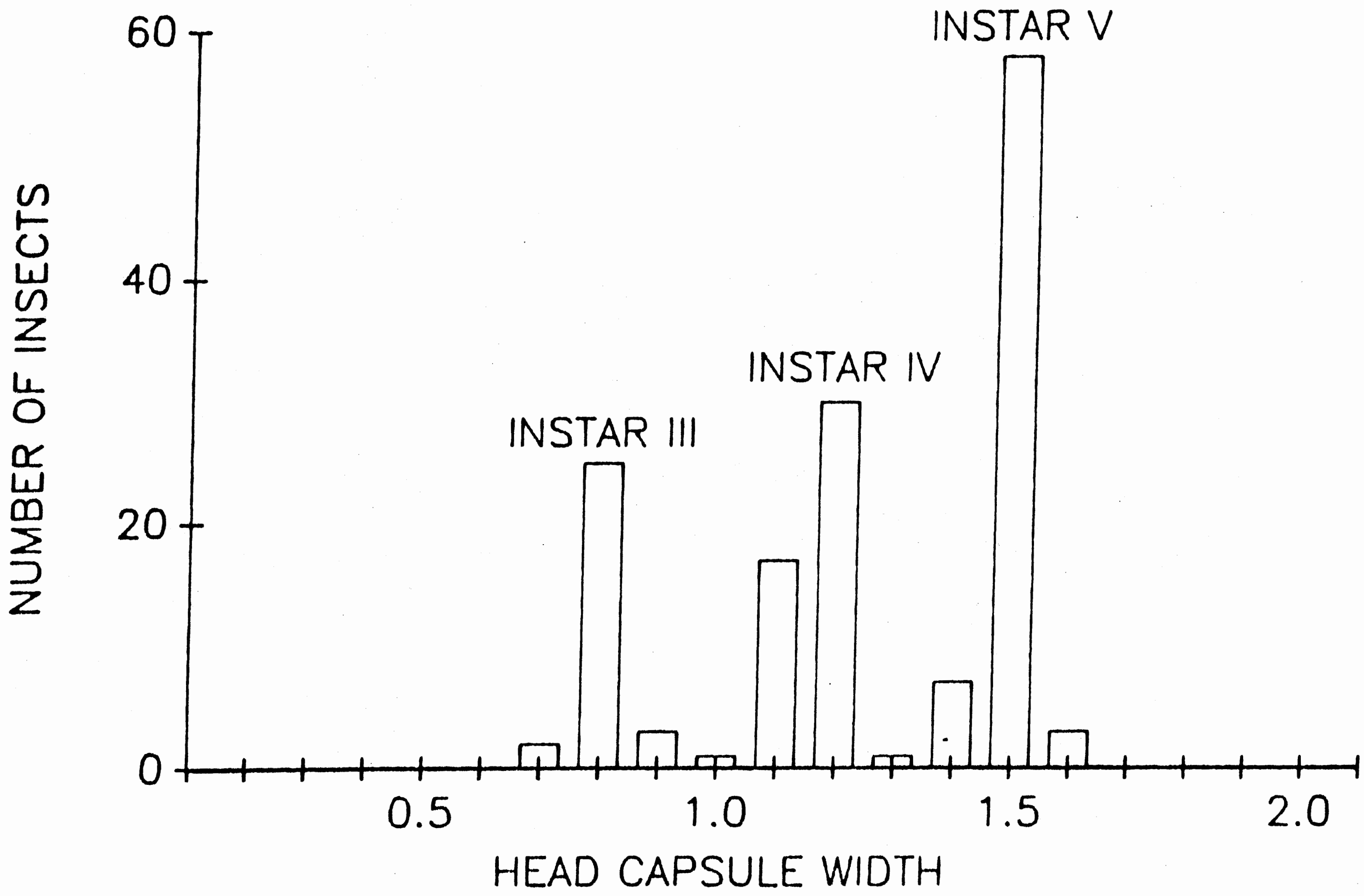

Figure 5. Length Frequency Histogram of <u>Asynarchus</u> Head Capsule Width.

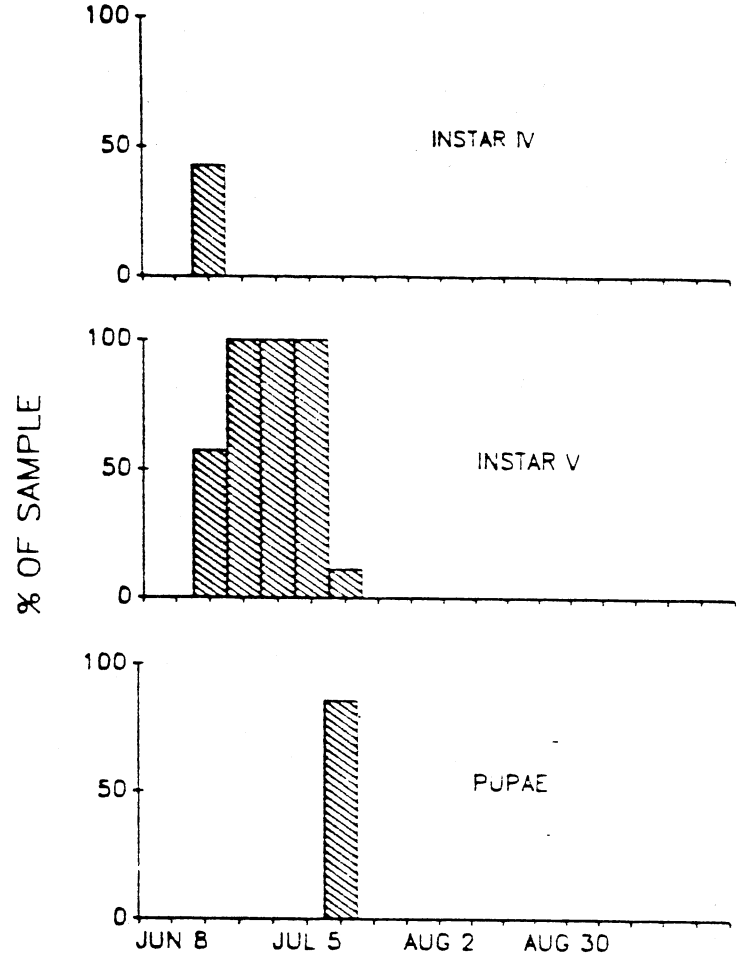

Figure 6. _Asynarchus_ development in 1987. Summary of Weekly Quadrat Samples.

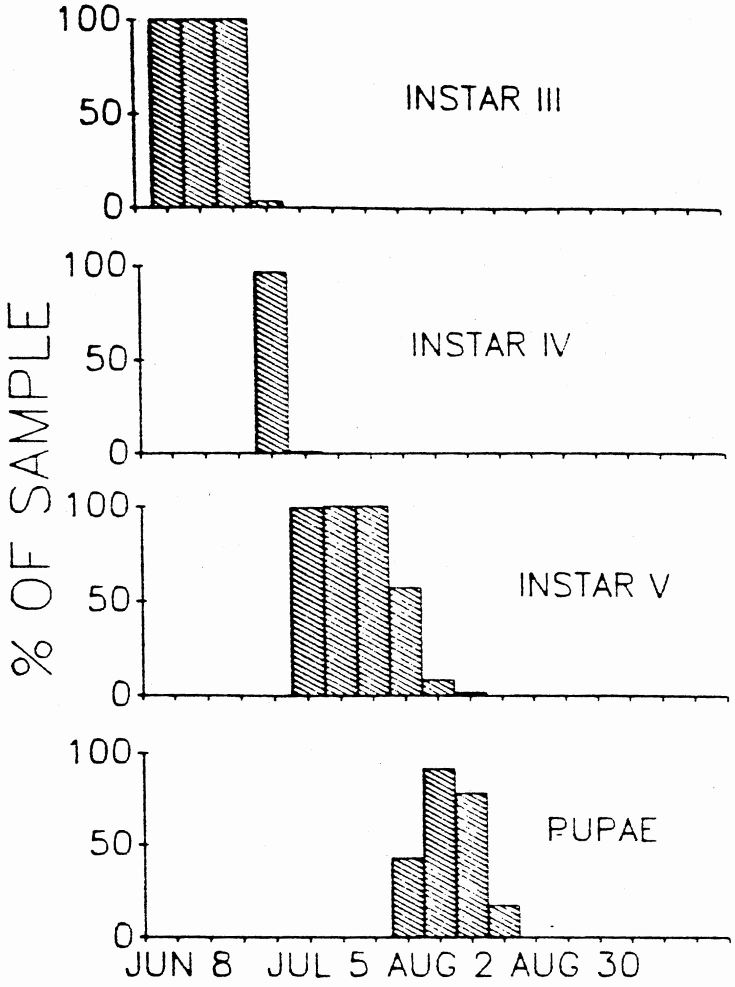

Figure 7. <u>Asynarchus</u> development in 1988. Summary of Weekly Quadrat Samples.

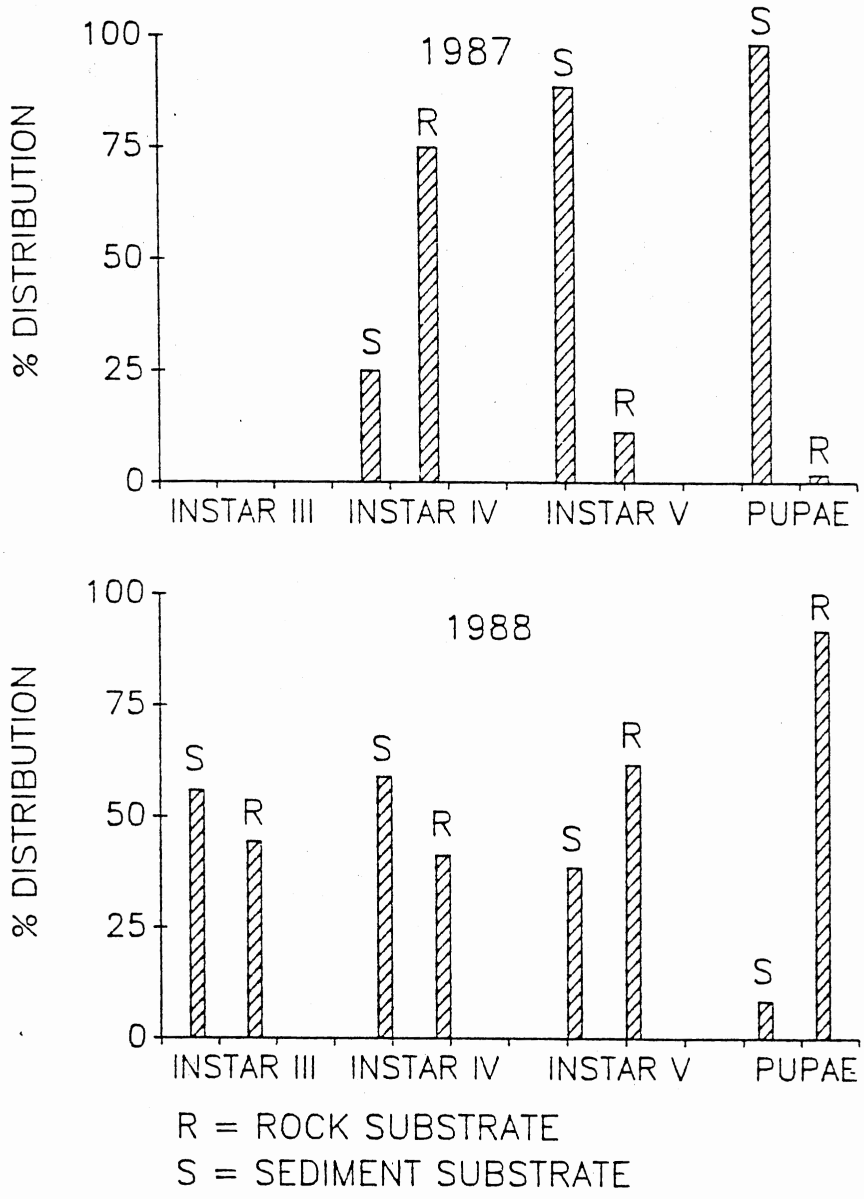

Figure 8. Asynarchus Larval and Pupal Distribution on Substrate in 1987 and 1988.

Aquatic Insect Emergence

During 1988 *Asynarchus* sp. emergence began 2 wk later than in 1987 (Figure 9). This is similar to seasonal patterns in *Asynarchus* sp. larval development.

Chironomid emergence began from 1 to 3 wk later in 1988 than in 1987 in all species except *Orthocladius* sp. 2. *Orthocladius* sp. 1 emerged in July and sp. 2 emerged in August and September (Figure 10). *Orthocladius* spp. was the most dominant taxa found in emergence traps. Emergence of all other aquatic insects in the wetland was somewhat later during 1988 than 1987. Animals collected in the emergence traps at a rate of less than 1 insect per trap per week are reported in Table 2.

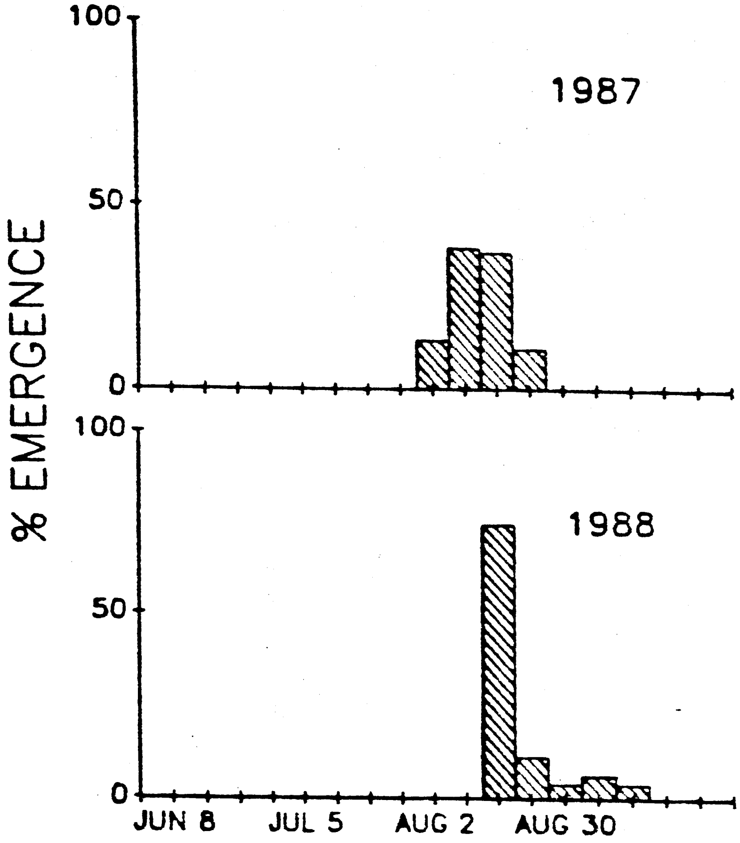

Figure 9. *Asynarchus* 1987 and 1988 Adult Emergence.

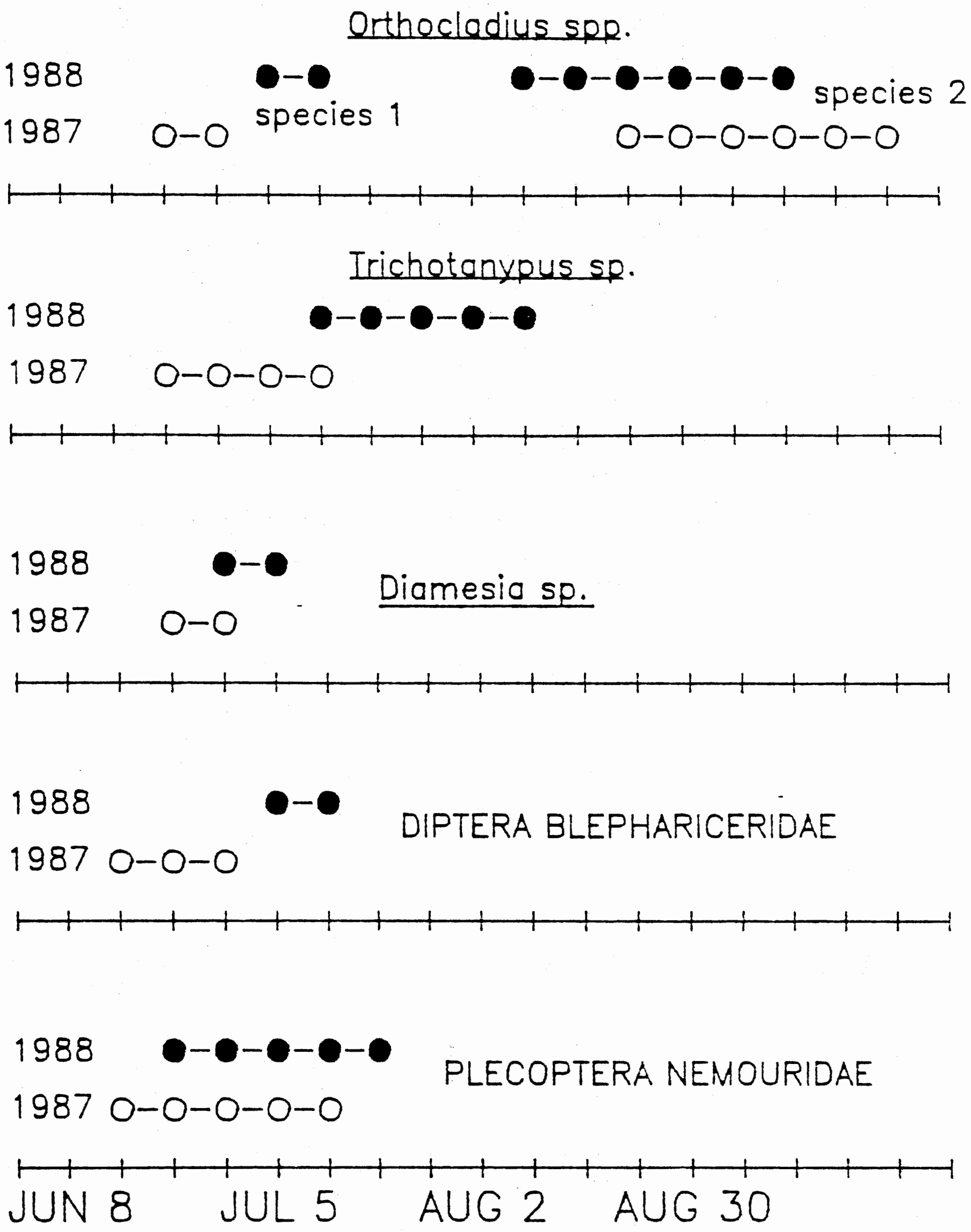

Figure 10. Chironomidae, Blephariceridae, and Nemouridae Emergence Patterns for 1987 and 1988. Connected Circles Indicate Continued Emergence.

Aquatic Insect Food Habits

Food ingested by <u>Asynarchus</u> sp. was largely detritus and occasionally diatoms. All instars had essentially the same food habits. All Chironomid species occupy the trophic relationship of collector-gatherer (Merritt & Cummins 1984) (Table 6). All used detritus, diatoms, and algae as food except <u>Pseudodiamesia</u> sp. which ate only algae. All also ate autotrophic matter and food not recognizable as diatoms or algae.

TABLE 6

WETLAND DIPTERAN FOOD HABITS

TAXA (Trophic Relationship)[a]	PRESENCE (+) OR ABSENCE(-) IN GUT CONTENTS			
	DIATOMS	ALGAE	DETRITUS	OTHER
Microspectra sp. (collector-gatherer)	+	-	+	+
Orthocladius spp. (collector-gatherer)	+	-	+	+
Phaenospectra sp. (scraper-collector-gatherer)	-	+	-	+
Trichotanypus sp.	+	-	+	+
Pseudodiamesia sp. (gatherer)	-	+	-	+

[a] from Merritt & Cummins (1984)

OTHER = All autotrophic material not recognizable
as diatoms or algae.

CHAPTER V

DISCUSSION

Climate and Phenology

Temperatures observed during spring 1987 in the Green Lakes Valley were higher than those observed during the spring of 1988. This early spring warming during 1987 is thought to have resulted in earlier ice melt and spring runoff. Wetland sediment temperatures indicated earlier ice melt and spring runoff in 1987 (Figures 3 and 4). The seasonal difference between 1987 and 1988 in wetland temperature seems to have affected the seasonal timing of aquatic insect life cycle events.

The seasonal timing of instar molts and pupation in Asynarchus was different between 1987 and 1988 (Figures 6 and 7). This phenology relates to the wetland temperature patterns of both years. Warm temperatures early in 1987 are believed responsible for growth and development beginning earlier than in 1988. This appears to be reflected in all Asynarchus sp. life stages in 1987.

Comparison of chironomid adult emergence between 1987 and 1988 showed a later emergence period for all species in 1988, with one exception. This seasonal difference seems to be controlled by the temperature. Temperature in the sediment first reached 4 degrees Celcius 1 month earlier in 1987 than 1988 (Appendix A). If the threshold for pre-emergence development is 4 degrees Celcius (Danks and Oliver 1972), then the difference between years in temperature could account for seasonal emergence patterns observed for most chironomidae.

Orthocladius sp. 2 emergence was later in 1987 than 1988. Thus, it did not exhibit the same timing of emergence as other wetland species. Sp. 2 emergence did not appear to be triggered by the spring thaw in the wetland. The emergence of Orthocladius sp. 2 in August and September is the only fall emergence period reported for any wetland insect. Fall emergence was not related to spring temperatures. Thus, similar phenology to other wetland insects would not be expected.

Life History

Chironomid Distribution and Diversity

Core sampling during June, 1987, in the wetland proved useless in determining chironomid age distribution as no organisms of any kind were obtained. The chironomid larvae are assumed to have been in overwintering condition when the core samples were taken. The overwintering behavior of most cold environment larvae is unknown. Although no larvae were collected in the wetland sediment to 10 cm depth, these larvae may have overwintered in deeper sediment.

Chironomid spatial distribution from substrate samples taken in the fall indicates a higher number of species and species diversity in the outlet region of the wetland during both years. Higher species diversity was found particularly in the Brillouin, Simpson, and Shannon indices which reflect dominance diversity (Wilhm 1972 and Perkins 1981). The Margalef and Mehinick indices are species richness indices (Wilhm 1972) and reflect the higher diversity in the outlet region, but not with the magnitude of the dominance indices. Dominance diversity indices are better measures of diversity in the wetland because they are less affected by sample size variability (Wilhm 1972). The average number of individuals on artificial substrate samples ranged from 15 to 173.

High outlet pool insect diversity, coupled with high numbers of emerging insects in the outlet pool (personal observation), demonstrates increased insect abundance in the outlet pool. This pattern of distribution in the wetland is related to a temperature gradient that existed from the inlet to the outlet. The inlet was approximately 2-3 degrees Celcius colder than the outlet throughout the growing season (unpublished LTER data).

This temperature gradient may result from the melt water from the rock glacier warming as it flowed from the inlet, through the pools (A,C,D), and to the outlet. Warmer temperatures in the outlet may support a larger assemblage of macroinvertebrates.

Asynarchus Distribution

Asynarchus sp. temporal distribution indicated a similar pattern of larval development in both 1987 and 1988. Instar V larvae were present in the wetland for 3 wk before pupation in both years. An insect with five life stages would require 18 weeks for development from egg to adult, if there were 3 weeks between molts. *Asynarchus* has a univoltine life cycle in the wetland. Thus, it appears capable of faster growth than that observed. This longer life cycle strategy is a result of the short (4 month) growing season in the wetland.

Asynarchus sp. microdistribution on the outlet pool substrate was not consistent between 1987 and 1988. Pupae were found on the sediment substrate in 1987 and on the rock substrate in 1988. Movement to rock substrate just prior to pupation seems more plausible since the larvae are collecting small stones from the rock substrate for their pupal case. The temperature patterns between the two years may have caused 1987 larvae to pupate before they could move to rock substrate. Early season growth in 1987 could have put the larvae in a later life stage than normal for the season. Further study is needed to determine Asynarchus sp. life stage substrate preferences.

Food Habits

Food habits in the wetland indicate two major food chains (Figure 13). The detrital food source was present throughout the season supporting the univoltine Asynarchus. Herbivorous chironomidae apparently rely on the primary production in the wetland for food (Coffman 1971). Algae and diatoms were never noticed early in the growing season but considerable periphyton growth was noted in August and September. Chironomid larvae were never collected early in the season and were assumed to be in overwintering condition until their presence was observed in the wetland pools. Chironomid larval activity in the wetland pools usually coincided with "greening" of these pools in August. These larvae appear to become active in the wetland at the time of food availability.

The life cycles of Microspectra sp., Phaenospectra sp., Pseudodiamesia sp., and Trichotanypus sp. appear to be designed to use the periphyton food source later in the growing season. Early summer emergence allows larvae to feed in the fall. The larvae have a limited time

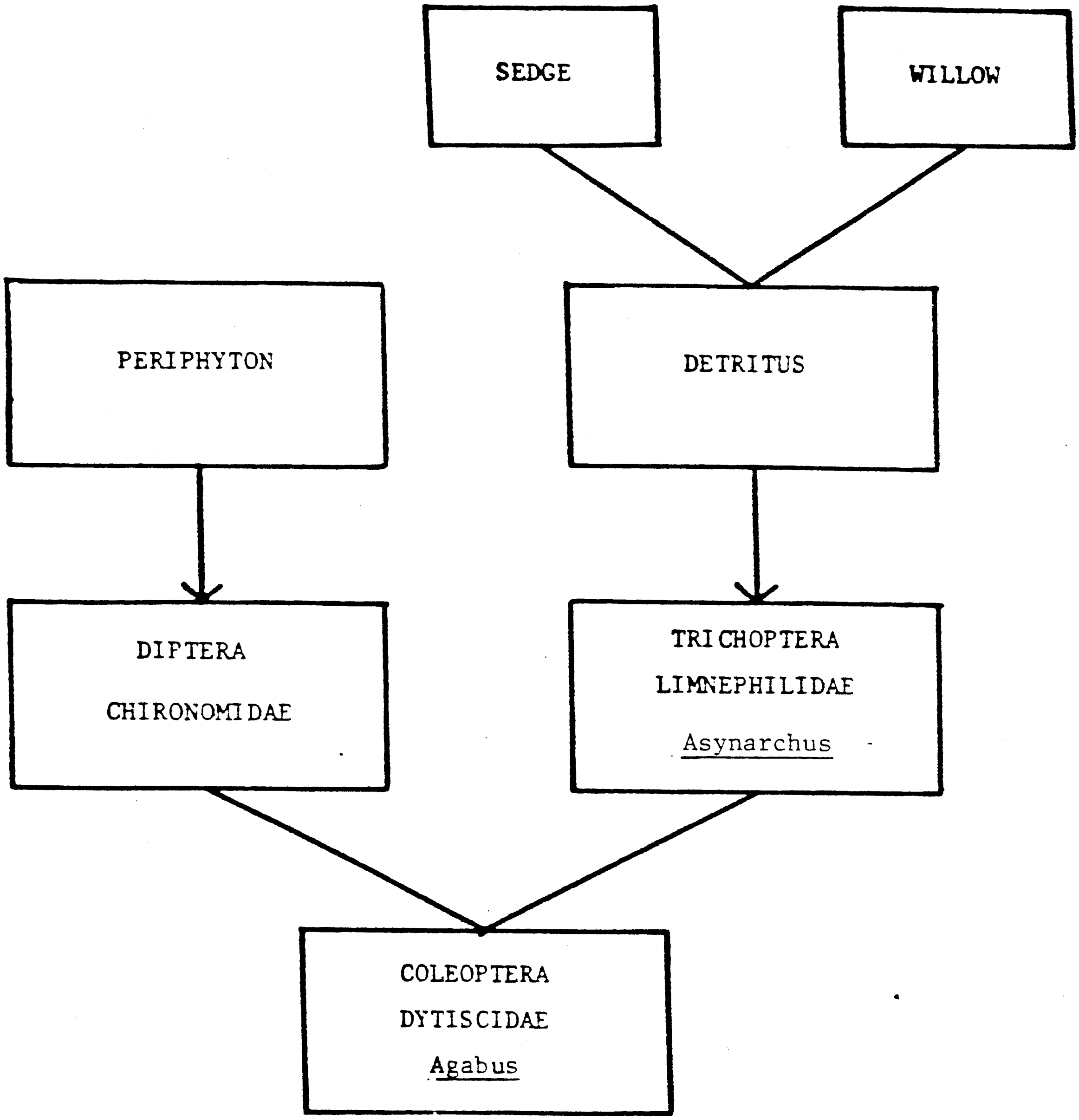

Figure 11. Detritus and Periphyton Food Chains in the Alpine Wetland. Primary Consumers are Chironomidae and <u>Asynarchus</u>.

period each year for growth and feeding and must be at the proper stage of development at that time to maximize their food source.

Orthocladius sp. 2 is the only insect that emerges during September when food is most available. Emergence during the time of periphyton growth seems unusual since all other chironomidae emerge early in the season. Sp. 2 could use detritus as a major component of its diet, allowing annual feeding and growth, but whether it does is unknown. Detritus feeding in this insect would explain the fall emergence pattern. Fall periphyton feeding would be uneccessary if periphyton were not a major dietary component.

Life Cycles

Multi-year life cycles have been reported in the arctic (Butler 1982, Downes 1965), especially for chironomidae. The five Chironomid species collected in the wetland are not among the common arctic species with a multi-year life cycle. The dominant chiromomid in the wetland (Orthocladius spp.) has been reported as univoltine in Alaska (Hershey et. al. 1988) and in this study. The presence of a multi-year life cycle strategy is apparently a species specific phenomenon in cold environments.

Conclusion

Wetland species were dominated by dipteran (*Orthocladius* spp.) and trichopteran (*Asynarchus* sp.) species. The wetland food web was characterized by detrital and herbivorous food chains. Chironomidae were herbivorous while *Asynarchus* sp. fed mostly on detritus.

The five chironomid species and *Asynarchus* sp. all appear to be univoltine. Life cycles of most wetland insects exhibited a phenology that relates to climate. Early spring warming in 1987 seems to have caused life cycle events such as molting and emergence in all species to occur earlier than in 1988. Climatic patterns early in the year apparently determined the seasonal timing of most life stages of most species except *Orthocladius* sp. 2. The outlet pool contained the highest insect diversity and abundance.

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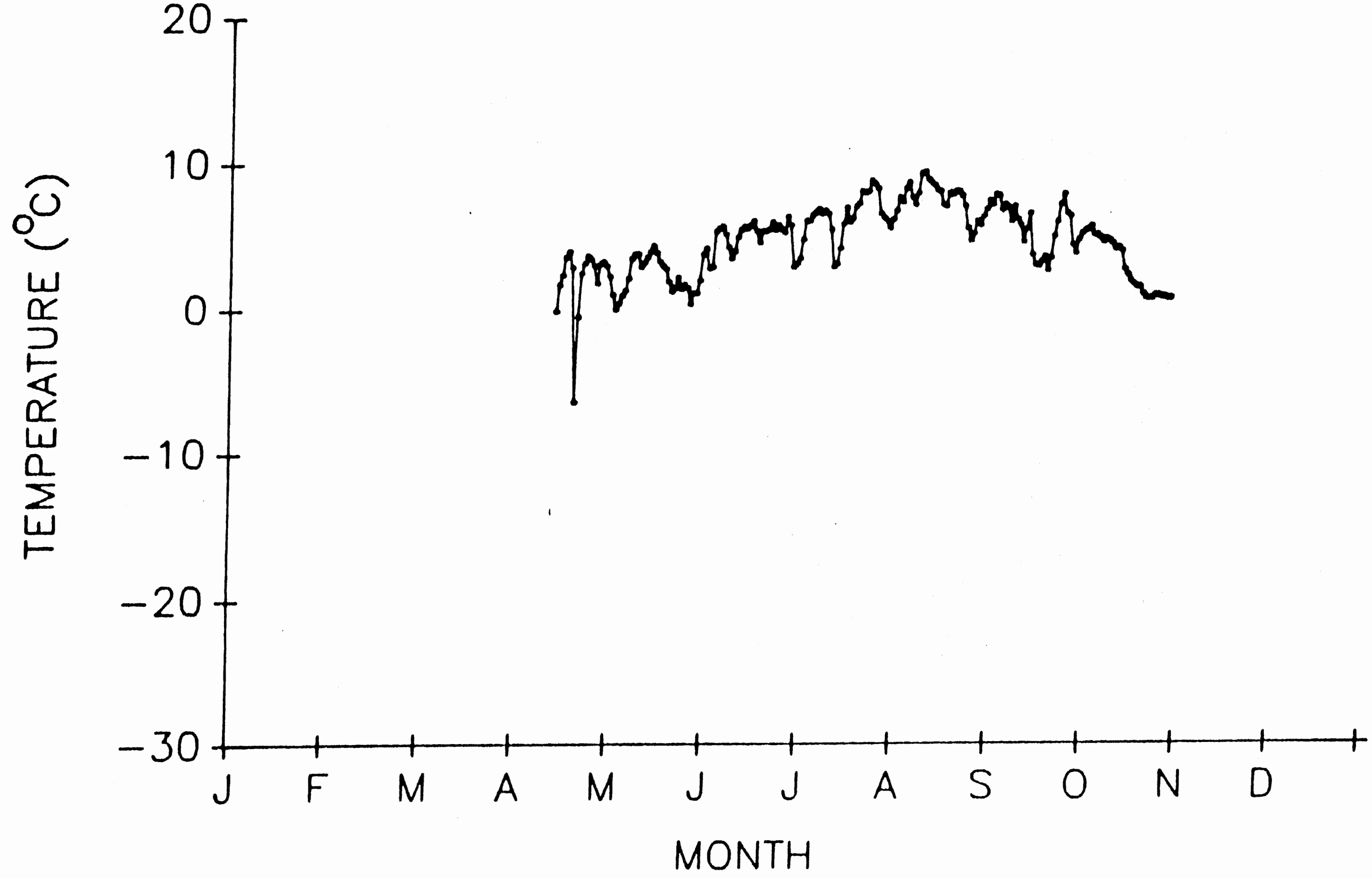
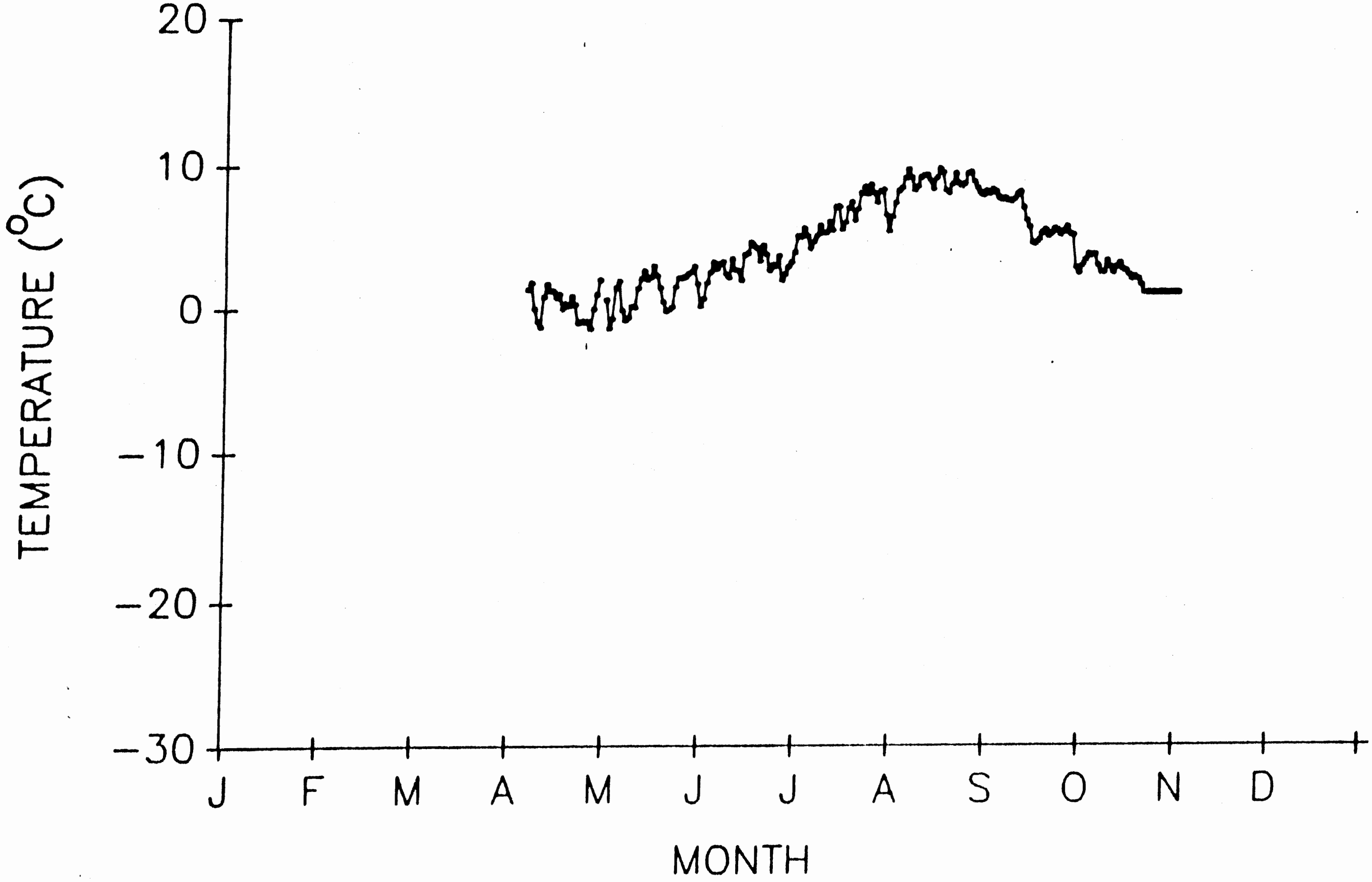
APPENDICES

APPENDIX A

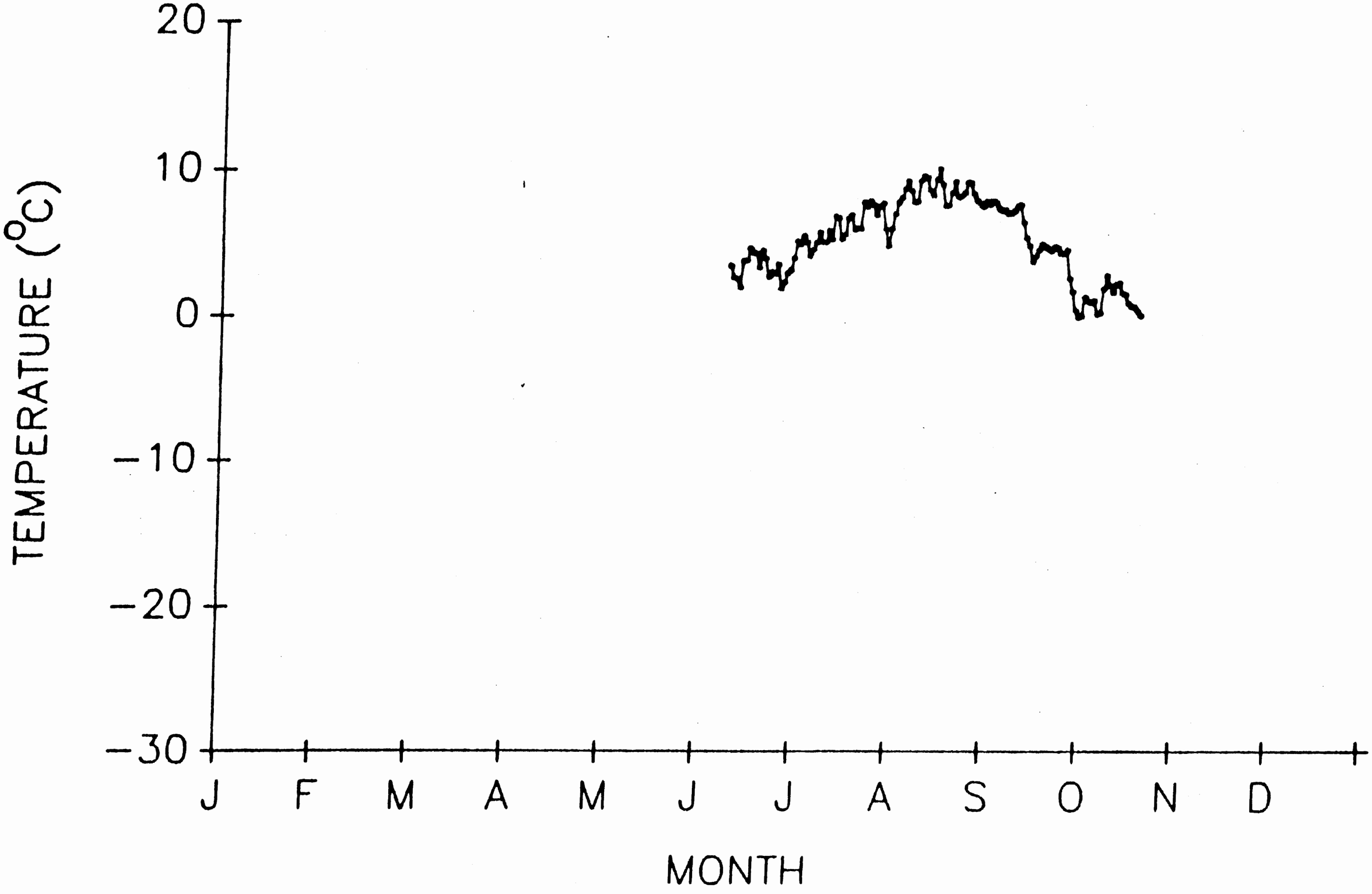
WETLAND SEDIMENT DAILY AVERAGE TEMPERATURES
FOR 1987 AND 1988



Daily Average Temperature in the Wetland Outlet Pool Sediment (10 cm Depth) for the 1987 growing season.



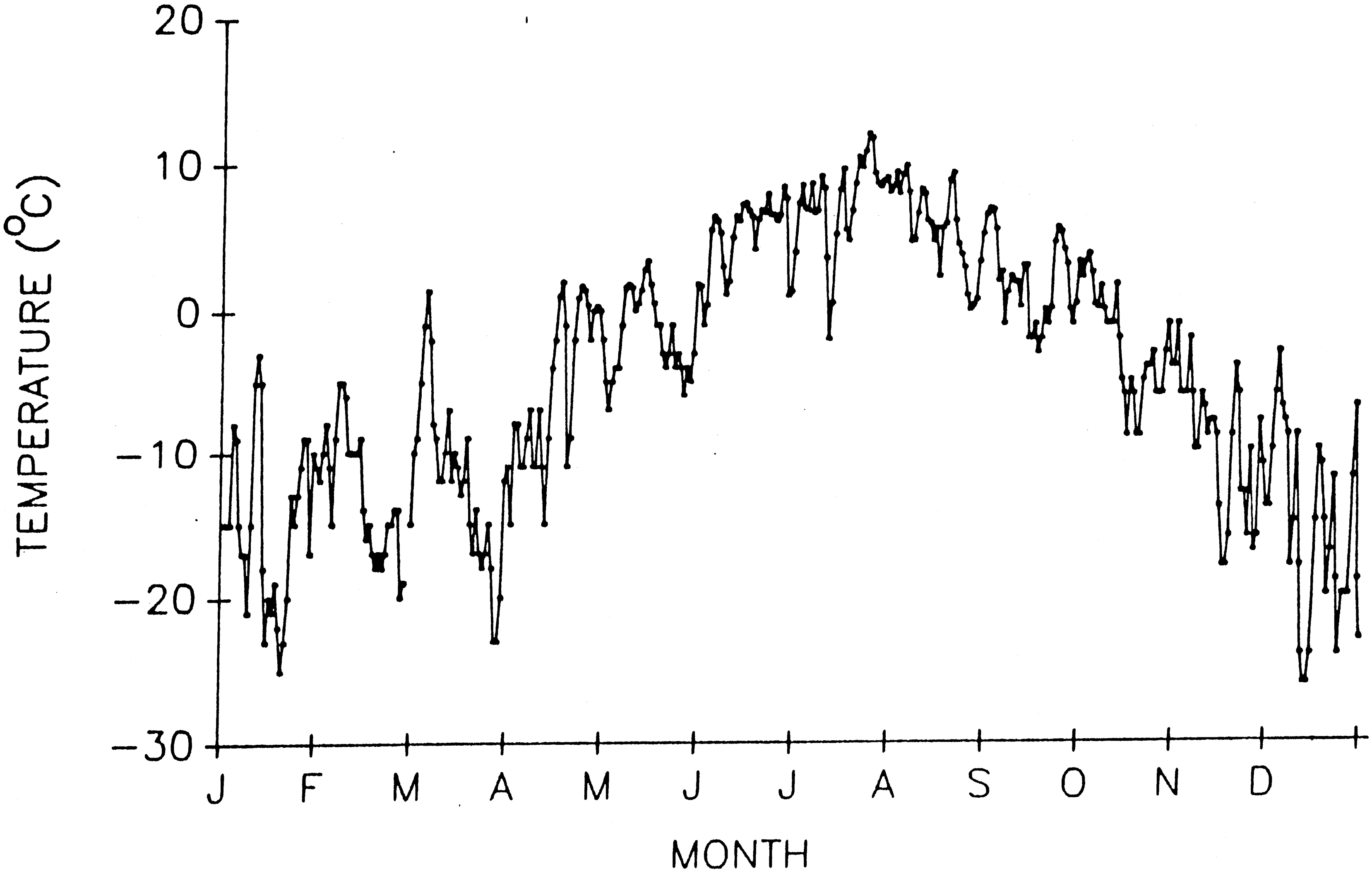
Daily Average Temperature in the Wetland Outlet Pool Sediment (10 cm Depth) for the 1988 growing season.



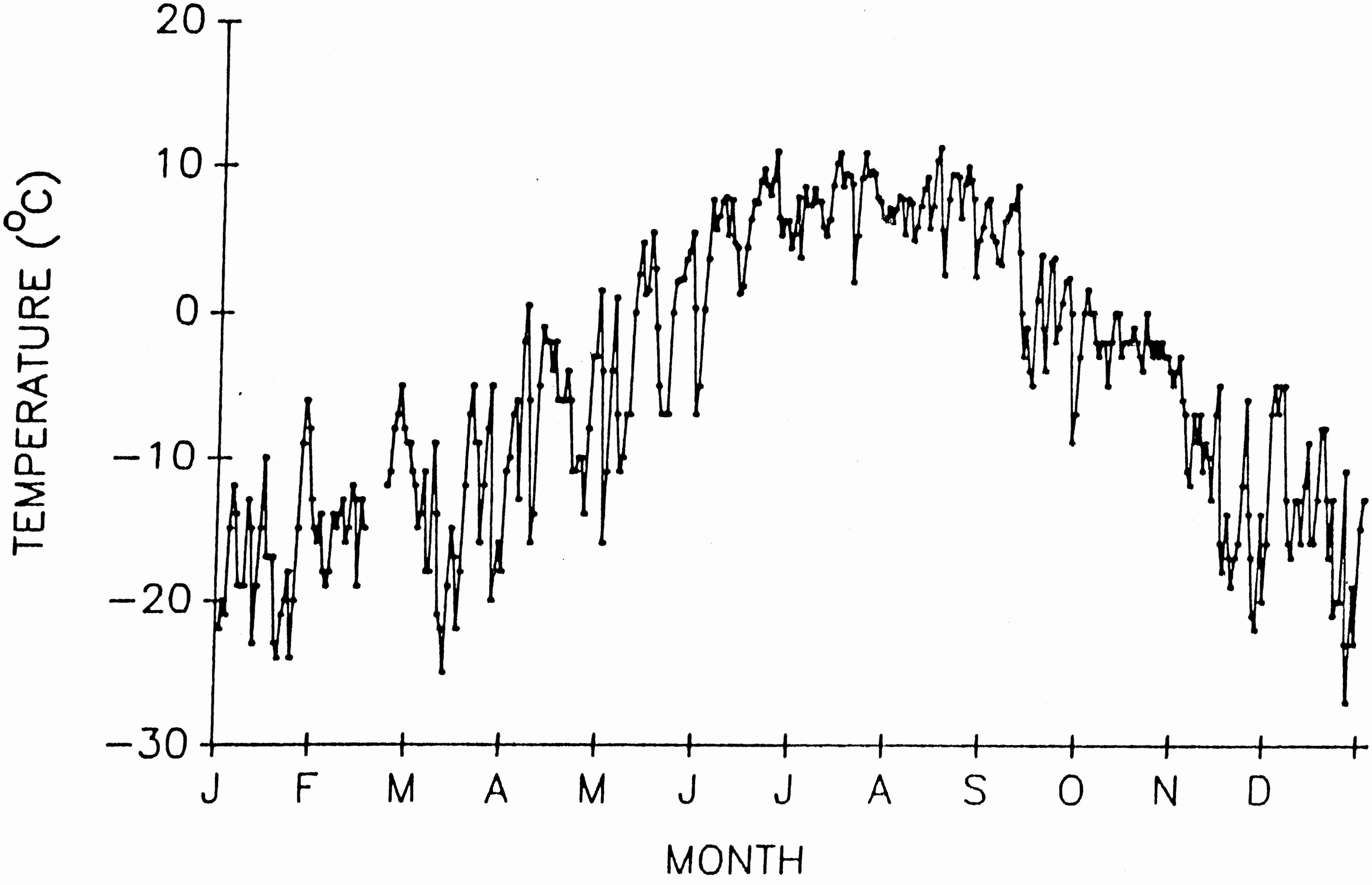
Daily Average Temperature in the Wetland Outlet Pool Sediment surface for the 1988 growing season.

APPENDIX B

ARIKAREE WEATHER STATIONS DAILY AVERAGE TEMPERATURES FOR 1987 AND 1988



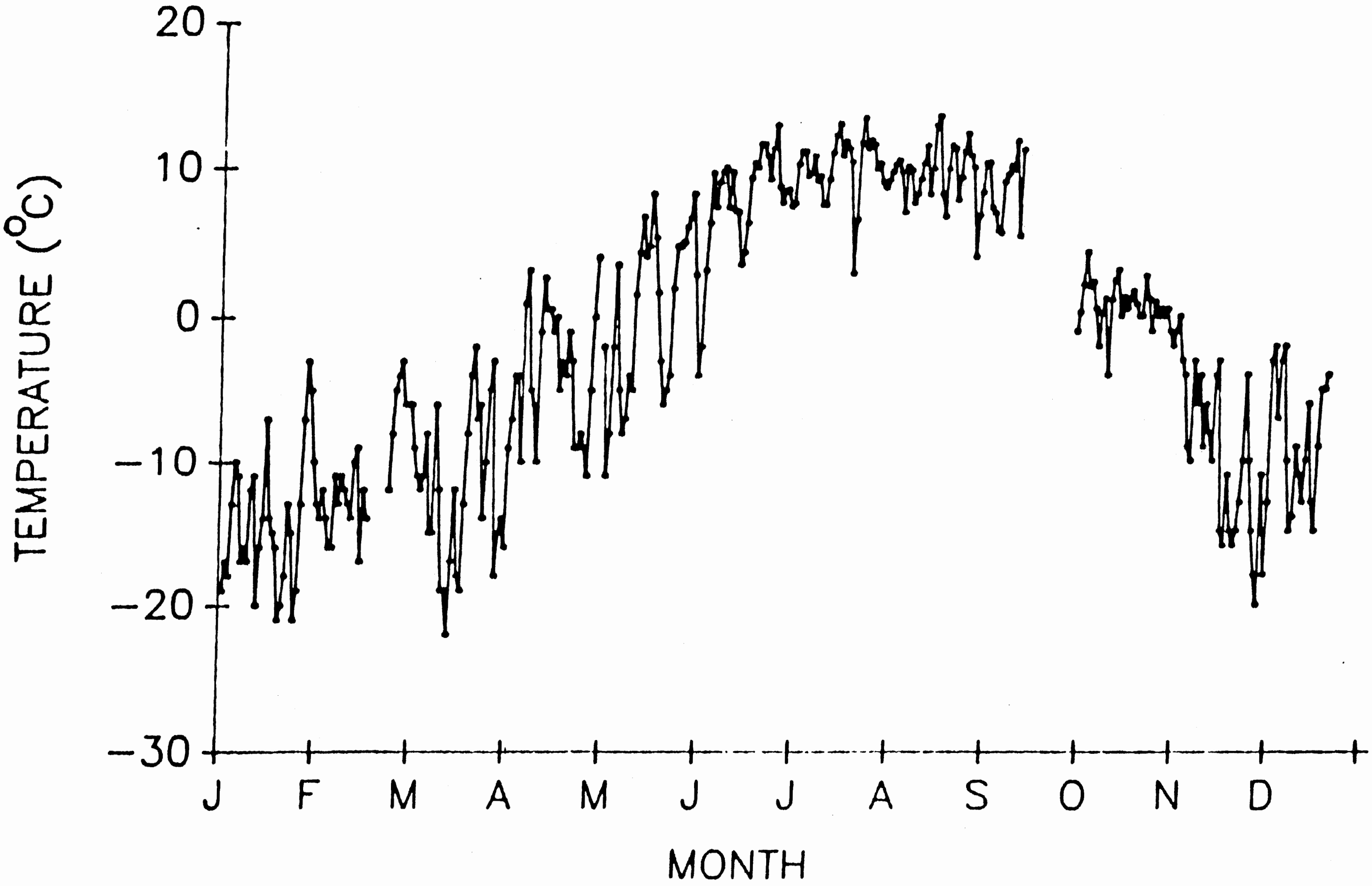
Daily Average Air Temperature for 1987 at the Arikaree Weather Station



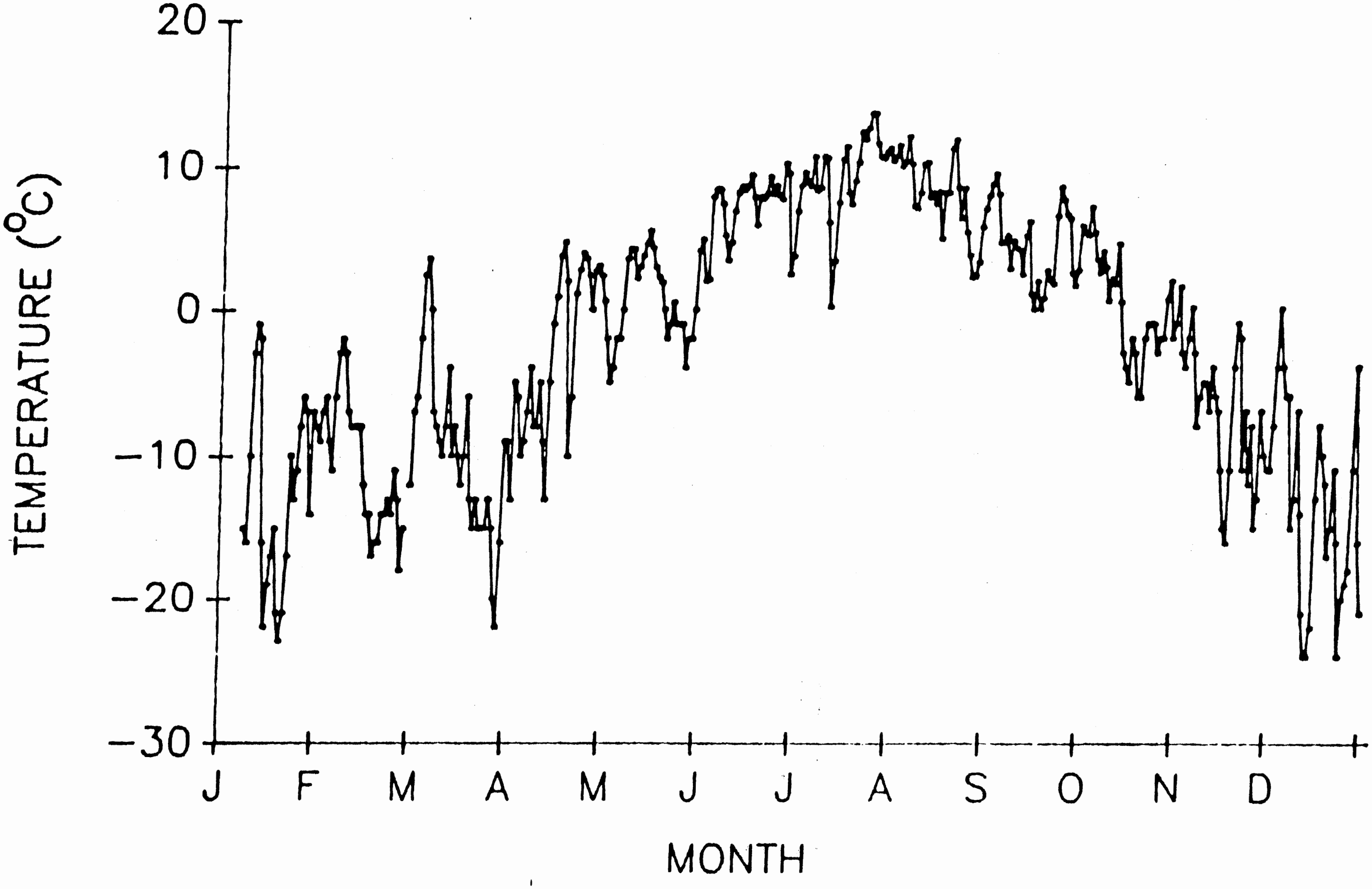
Daily Average Air Temperature for 1988 at the Arikaree Weather Station

APPENDIX C

GREEN LAKE 4 DAILY AVERAGE TEMPERATURES FOR 1987 AND 1988



Daily Average Air Temperature for 1988 at the Green Lake 4 Weather Station



Daily Average Air Temperature for 1987 at the Green Lake 4 Weather Station

APPENDIX D

TOTAL CUMULATIVE DEGREE DAYS BY MONTH FOR 1987 AND 1988 IN THE GREEN LAKES VALLEY[a]

MONTH	G-4 1987	G-4 1988	ARIK 1987	ARIK 1988	Wetland 1987	Wetland 1988
JAN	0	0	0	0	0	0
FEB	0	0	0	0	0	0
MAR	6.0	0	1.4	0	0	0
APR	33.5	11.7	7.7	2.0	41.7	13.9
MAY	48.7	79.6	17.1	39.8	66.4	38.9
JUN	212.5	245.2	193.8	180.6	150.0	100.0
JUL	298.6	311.2	232.3	239.7	194.4	198.8
AUG	246.2	296.8	173.2	227.4	232.6	268.5
SEP	132.1	166.4	63.8	74.9	182.7	179.8
OCT	49.3	30.6	15.6	3.5	84.6	59.5
NOV	1.6	0	0	0	0	0
DEC	0	0	0	0	0	0

[a] ARIK = Arikaree weather station
G-4 = Green Lake 4 weather station

APPENDIX E

1987 SUBSTRATE SAMPLING RESULTS[a]

sample date(site)	OR	MS	PH	PS
8-24-87(outlet)	52	11	6	2
8-24-87(outlet)	92	8	2	
8-24-87(pool D)	40	9		
8-24-87(pool B)	75			
8-24-87(pool B)	50		1	
9-16-87(outlet)	5	8	1	2
9-16-87(outlet)	12	1	1	1
9-16-87(pool D)	16	6	1	
9-16-87(pool D)	13			

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[a] Number by taxa per substrate sampler is shown.
OR = Diptera Chironomidae _Orthocladius_
MS = Diptera Chironomidae _Microspectra_
PH = Diptera Chironomidae _Phaenospectra_
PS = Diptera Chironomidae _Pseudodiamesia_

APPENDIX F

1988 SUBSTRATE SAMPLING RESULTS[a]

sample date(site)	OR	MS	PH	PS	TR
8-18-88(outlet)	89		1	9	2
8-18-88(outlet)	12		30		
8-18-88(outlet)	8	16	1		
8-18-88(outlet)	11		2	9	2
8-18-88(outlet)	40		5		
8-18-88(pool D)	32		19	1	
8-18-88(pool D)	30		21	2	
8-18-88(pool D)	10		3		
8-18-88(pool B)	41	31	27		
8-18-88(pool B)	4		12	20	
8-18-88(pool B)	56	12	7		
8-18-88(pool A)	132	50	18		
8-18-88(pool A)			6	18	
8-18-88(pool A)		1	11	18	
8-18-88(pool A)			21	26	
9-12-88(outlet)	21	10	9	1	1
9-12-88(outlet)	15	5	5	2	
9-12-88(outlet)	15	10	1	1	1
9-12-88(outlet)	4	5	11		
9-12-88(outlet)	5	4	9		
9-12-88(pool D)	4	1	3	1	
9-12-88(pool D)	18		7	1	
9-12-88(pool D)	3	2	3		
9-12-88(pool D)	29		24	2	
9-12-88(pool B)	23		41		
9-12-88(pool B)	89	14	23	1	

[a] Number by taxa per substrate sampler is shown.
OR = Diptera Chironomidae *Orthocladius*
MS = Diptera Chironomidae *Microspectra*
PH = Diptera Chironomidae *Phaenospectra*
PS = Diptera Chironomidae *Pseudodiamesia*
TR = Diptera Chironomidae *Trichotanypus*

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