31 Subalpine Wetlands in Colorado

Habitat Permanence, Salamander Predation, and Invertebrate Communities

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Wetlands are abundant in wet subalpine and montane valleys on the western slopes of the Rocky Mountains. Although geological and vegetational characteristics are well studied for a diversity of wetland types and incorporated into a regional classification, there is a paucity of information about the invertebrates in these habitats and the factors that affect their distribution and abundance. In this chapter we report on work at a subalpine wetland complex in the Elk Mountains of central Colorado composed of numerous adjacent basins that vary considerably in size, depth, water chemistry, and hydroperiod. We identified over 100 planktonic and benthic invertebrates at the site and found that different basins have quite different species assemblages. We used comparative data on the abiotic environment (area, depth, hydroperiod, chemistry) in 40 basins and information about the density of tiger salamanders, the only vertebrate predator, to construct a path analytic model to explore hypotheses about the relative importance of these factors on invertebrate community composition. Basin area, hydroperiod, and salamander densities have significant and collinear effects on species diversity and community composition. Large, permanent basins with multiple year-classes of salamander larvae are most diverse and are dominated by small-bodied zooplankton, chironomid midges, small dytiscid beetles, and cased caddisflies. Semipermanent, autumnal basins are less diverse than permanent basins and dominated by species that are absent or rare in permanent basins (large-bodied cladocerans and copepods, fairy shrimp, large dytiscid bee-

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tles). In semipermanent basins beetles replace salamander larvae as the top predators on benthic invertebrates, although salamander adults and hatchlings remain the top predators on large-bodied zooplankton. Small, vernal basins lack salamanders and are dominated by a subset of autumnal-basin species (several zooplankton, mosquitoes, a beetle, a caddisfly, a corixid water boatman) that are able to complete development before they dry in early summer. Although a few species are restricted to permanent habitats because they cannot tolerate drying, most of the invertebrates in these wetland are physiologically capable of, and have life cycles amenable for, exploiting both permanent and nonpermanent basins. Thus, biotic interactions, especially the direct and indirect effects of salamander predation, are viable hypotheses for explaining patterns of invertebrate distribution and abundance along the permanence gradient from vernal to semipermanent to permanent wetland basins. Human activities that threaten salamander populations should have cascading effects on the invertebrate communities in permanent subalpine wetlands.

INTRODUCTION

Mountain valleys on the wet western slopes of the Rocky Mountains contain numerous wetlands that occur in a diversity of geomorphologic and hydrologic settings. For example, within just a few kilometers of our study site in central Colorado are, from high to low elevations, lacustrine marshes bordering alpine lakes (>3500 m), subalpine (2800–3500 m) ponds and fens in bedrock and soil depressions, subalpine riparian meadows, montane (2100–2800 m) beaver ponds and riparian willow thickets, and montane kettle ponds and fens in broad glacial valleys. The geological origins, hydrology, and vegetational characteristics of these and other types of montane and subalpine habitats have been used to construct a detailed classification system for the wetlands of the Rocky Mountain Region (see review by Windell et al. 1986). However, as is often the case in general treatments of wetlands ecology (see Batzer and Wissinger 1996), there is a paucity of information about invertebrate communities in all of the wetland types discussed in Windell et al. (1986). This is not an oversight—with the exception of several early studies by Pennak and his students (e.g., Neldner and Pennak 1955, Schmitz 1956; also see Blake 1945), there is little information about benthic invertebrates in Rocky Mountain wetlands. Similarly, with the exception of the zooplankton studies at our site (Dodson 1970, 1974, Sprules 1972, Maly 1973, Maly and Maly 1974, Maly et al. 1980, Willey and Threlkeld 1993), most research on high-elevation zooplankton assemblages has focused on deep alpine lakes (e.g., Larson et al. 1996 and references therein).

In this chapter we focus on the invertebrate communities in a complex of subalpine ponds located near the Rocky Mountain Biological Lab (RMBL) in Gunnison Co., Colorado. We first describe the habitat characteristics (geomorphology, hydrology, chemistry, plant structure, salamander predators) of the many small basins at our study site. We then discuss the invertebrate fauna and patterns of distribution and abundance among basins. We use path analysis to help disentangle the collinear relationship among the various habitat variables and to compare hypotheses about how those variables directly or indirectly affect invertebrate community composition. Finally, we discuss the results of previous experimental work conducted at this study site (Dodson 1970, 1974, Sprules 1972, Wissinger et al. 1996, Wissinger et al., 1999) that examined how different habitat factors affect the distributional patterns for several of the dominant taxa in these communities.

HABITAT DESCRIPTION

Our study site is located in the Mexican Cut Nature Preserve (MCNP), a 960-acre inholding within the White River National Forest that is owned by The Nature Conservancy and managed by the RMBL for ecological research. The wetlands occur at or just below tree line (3400–3500 m elevation) on two flat shelves on the northeast slopes of Galena Mountain in Gunnison Co., Colorado (Fig. 31.1). Although many of the basins at Mexican Cut are only a few meters or tens of meters apart, they often contain quite distinct assemblages of invertebrates. Because all of the basins occur at about the same elevation and have the same macroclimate and the same pool of potential colonists, the site provides an excellent ecological setting for isolating the effects of basin characteristics (area, size, hydroperiod, water chemistry) on community composition. These wetlands typify many of the other subalpine habitats that we have been studying in this region in terms of their abiotic setting, the surrounding terrestrial habitat, and the dominant aquatic flora and fauna.

Bedrock and Water Chemistry

There are over 50 small (10 m^2–4682 m^2 surface area), shallow (0.3–2.5 m depth) basins in the wetland complex at MCNP (Fig. 31.1, Table 31.1). The site is underlain by upper Paleozoic rocks, and basins in the main cluster on the lower shelf lie on contact-metamorphosed sandstone (quartzite) that provides no source of alkalinity (99 percent silica) (Prather 1982). Thus, the water is extremely soft and poorly buffered in most basins (Table 31.2; Dodson 1982, Harte et al. 1985), as is generally true in the region (e.g., Neldner and Pennak 1955, Schmitz 1956, Landers et al. 1987). All basins are extremely oligotrophic, with total nitrogen and phosphorus concentrations typically below detection limits (<1 $\mu g/l$; conducted at USDA Forest Service

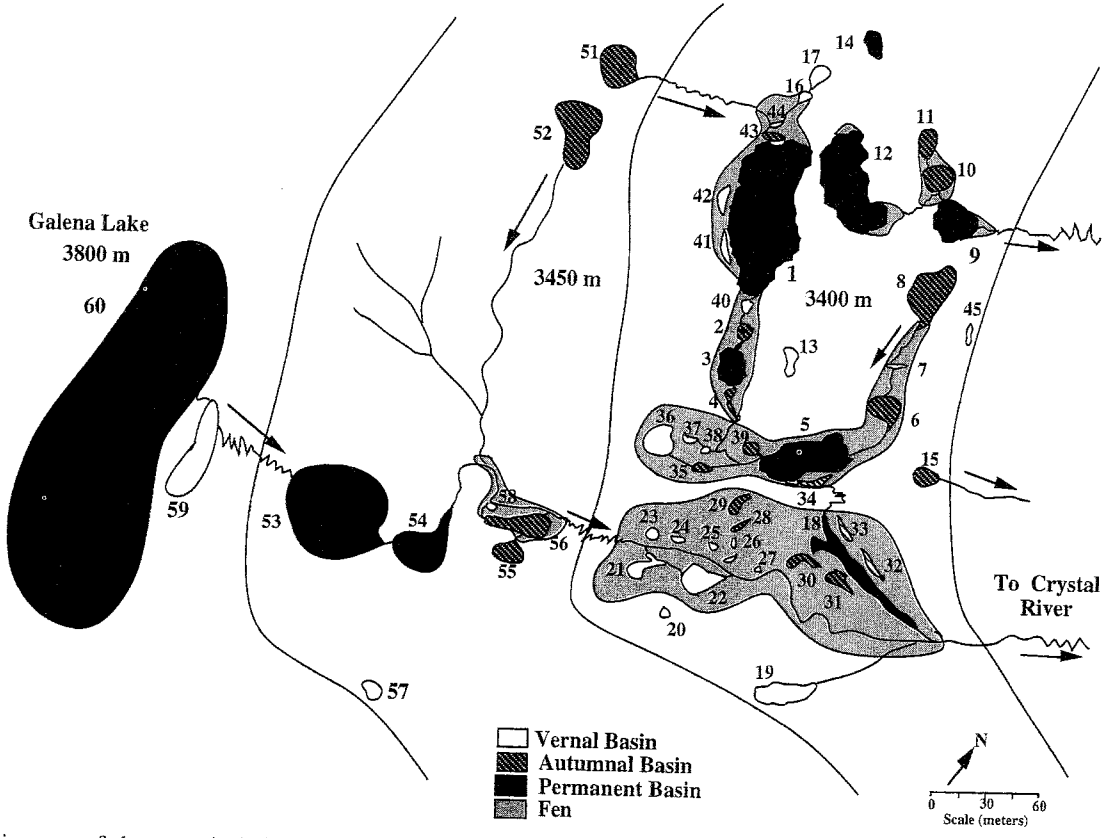


Fig. 31.1. Schematic map of the aquatic habitats at the Mexican Cut Nature Preserve. The three vertical contour lines separate from right to left, the lower cut at 3400 m, the upper cut at 3450 m, and Galena Lake at 3800 m elevation.

TABLE 31.1. Basin Characteristics (Area, Depth, Hydroperiod) and Invertebrate Community Composition for 41 Wetland Basins at the Mexican Cut Nature Preserve[a]

Basin	20	22	42	44	23	41	13	16	36	19	25	21	24	7	26	37	15	38	29	39	27	43	35	30	31	28	4	51	52	55	56	6	8	10	11	2	3	9	5	12	1
Area (m^2)	16	90	25	20	18	25	89	30	400	230	15	160	44	37	12	18	64	10	64	20	28	60	20	22	10	12	30	600	750	400	750	206	928	283	213	15	175	585	1267	1688	4632
Depth (m)	0.3	0.3	0.3	0.5	0.3	0.3	0.3	0.6	0.5	0.6	0.5	0.5	0.3	0.3	0.5	0.8	0.6	0.4	0.6	0.5	0.5	0.8	0.5	0.5	0.5	0.7	0.8	0.7	0.7	1.0	0.7	1.2	0.7	1	1	1	1.5	1.5	1.5	2.0	2.5
Wet (open water days)	40	41	42	51	56	58	58	59	59	59	59	61	63	63	64	64	74	74	75	76	81	84	85	88	88	89	99	100	102	104	105	110	112	114	115	116	130	140	138	135	135
	← Vernal →																← Autumnal →																					← Permanent				
Keratella	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
Stictotarsus	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
Tanytarsus	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	R	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
Asynarchus		R	R	C	R	R	R		C	C	C	C	C	C	C	C	C	C	R	C	R	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	R	R	C
L.coloradensis		C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
Aedes spp.		C	C	C	C	C	C	C	C	C	C	C				R		C																							
Arctocorixa			C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C			R			
C. riparius				C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C		C	C	C				R	R	R
Acanthocyclops					C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
D. middendorfiana							C		C	C	C	C	C	C	C	C	C	C	C	C	C	C	C		C	C	C	C	C	C	C	C	C	C	C				R		
Branchinecta							C	C	R	C	C	C		C	C		C	C								C	C	C	C	C	C	C	C	R	R	R					
Paratanytarsus							C		C	C	C	C	R	C			C	C	C		C					C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
Psectrocladius							C		C	C	C	C					C	C	C	C		C					C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
Conochilus							C	C	C	C		C					R	C									C	C	C	C	C	C	C	C							
Euchlanis							C	C	C	C		C					C	C				C					C	C	C	C	C	C	C	C				C	C	C	C
Limnophila									R									R	R																						
Lumbricolus									R	R		R				C	C	C	C	C	C	C		C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
Sanfilippodytes																		R		R				R				C	C	C	C	C	C	C	C	C					
Hydropous																	R					R						C	C	C	C	C	C	C	C						
Chydorus																	R					R						R	R	R	R	R	R	R	R	C	C	C	C	C	C
Limnephilus picturatus																	C		C		C		C	C														R	R		R
Simocephalus																	R	R		R		C	R	R			C	C	C	C	C	C	C	C	C	C	C	C	R	R	R
Chironomus salinarus																		R					C										C	C	C	C	R	C	C	C	C	C
Agabus kootenai																	C					C					C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
Limnodrilus																			C	R	C	R					C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
Callicorixa																						R						C	C	C	C	C	C	C	C	C	C	C	C	C	C
Gerris																						R					R	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
Pisidium																						R					C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C

TABLE 31.1. (Continued)

Basin	20	22	42	44	23	41	13	16	36	19	25	21	24	7	26	37	15	38	29	39	27	43	35	30	31	28	4	51	52	55	56	6	8	10	11	2	3	9	5	12	1
Area (m^2)	16	90	25	20	18	25	89	30	400	230	15	160	44	37	12	18	64	10	64	20	28	60	20	22	10	12	30	600	750	400	750	206	928	283	213	15	175	585	1267	1688	4632
Depth (m)	0.3	0.3	0.3	0.5	0.3	0.3	0.3	0.6	0.5	0.6	0.5	0.5	0.3	0.3	0.5	0.8	0.6	0.4	0.6	0.5	0.5	0.8	0.5	0.5	0.5	0.7	0.8	0.7	0.7	1.0	0.7	1.2	0.7	1	1	1	1.5	1.5	1.5	2.0	2.5
Wet (open water days)	40	41	42	51	56	58	58	59	59	59	59	61	63	63	64	64	74	74	75	76	81	84	85	88	88	89	99	100	102	104	105	110	112	114	115	116	130	140	138	135	135
	← Vernal →																← Autumnal →																				Permanent				
Hesperophylax																															R										
Agabus tristus																								R	R		R	C	C	C	C	C	C	C	C	C	C	C	C	C	C
Procladius																												C	C	C	C	C	C	C	C		R	R	R	R	R
Mesostoma																												C	C	C	C	C	C	C	C					R	
Helobdella																												C	C	C	C	C	C	R	C	C	C	C	C	C	C
Chydorus																												C	C	C	C	C	C	C	C		C	C	C	C	C
Cricotopus																												R	R	R	R	R				R	R		R		C
Limnephilus externus																														C	C	C	C	R	R	C	C	C	C	C	C
Agabus strigulosus																														R	R	R	R	C	C	C	C	C	R	R	R
Acilius																														R		R	R	R	R						
Dytiscus																														R	C	R	R	R	R			C			R
Somatochlora																														R	R	R	R	R	R		C	C	C	C	C
Limnesia																																		R		R	C	C	C	C	C
Piona																																			R	R	C	C	C	C	C
Bezzia																																				R	R	R	R	R	C
Nephelopsus																																					C	C	C	C	C
Agrypnia																																					C	C	C	C	C
Daphnia rosea																																					C	C	C		C
Scapholoberis																																					R	C	C	C	C
Lestes																																					C	C	C	C	C
Coenagrion																																					C	C	C	C	C
Plateumaris																																					R	C	C	C	C
Ilybius																																					C	C	C	C	C
Rhantus																																					R	R	R	R	R
Haliplus																																					R	R	R		R
Ablabesmyia																																					C	C	C	C	C
Culicoides																																					C	C	C	C	C
Cladopelma																																					C	C	C	C	C
Enallagma																																					C	C	C		C
Cladotanytarsus																																					C	C	C	C	C
Dicrotendipes																																					C	C	C		C
Endochironomus																																					C	C	C	C	C

Microtendipes																																					C	C	C	C	C
Pagastiella																																					C	C	C	C	C
Coryneura																																					C	C	C	C	C
Eukiefferella																																					C	C	C	C	C
Arrenurus																																					C	C	C	C	C
Lebertia																																					C	R	C	R	C
Hydrozetes																																					C	R	C	C	C
Glossiphonia																																					R	R	R	R	R
Daphnia pulex																																						R		C	R
Aeshna																																						R	R	R	R
Coenocorixa																																						R		R	R
Haliplus longullus																																						R	R	R	R
Hydrobious																																						R	R	R	R
Gyrinus																																								R	R
Callibaetis																																								R	C
Stenus																																								C	C
Pseudodiamesa																																									R
Notonecta																																									R
Stratiomyia																																									R
Helophorus																																									R
Basin #	20	22	42	44	23	41	13	16	36	19	25	21	24	7	26	37	15	38	29	39	27	43	35	30	31	28	4	51	52	55	56	6	8	10	11	2	3	9	5	12	1

[a] Area is maximum coverage (m^2) and depth is maximum depth (m) when the basins are filled. Wet represents the average number of ice-free days with water above the substrate. Vernal basins have dried every year between 1989 and 1996. Autumnal basins dry in most years but have remained wet in one to three of the years during this time period. Permanent basins have not dried in at least the last 50 years. C = commonly encountered and R = rare species. See Appendix 31.A for taxonomic affiliations.

TABLE 31.2. Water Chemistry Data for Select Basins at the Mexican Cut Nature Preserve for July 1993[a]

Basin	PH	Conduct. (μS/cm)	[μg/L] Al	[μeq/L] Ca	Mg	Na	K	NH4	Cl	NO3	SO4	PO4	Sum Bases	Sum Acids	Difference = alkalinity	ANC
1	7.27	35.19	23.47	303.59	90.52	9.48	2.53	0.00	1.41	0.00	53.93	0.00	406.12	55.34	350.79	286.70
2	6.96	29.89	19.41	254.34	77.93	5.87	1.13	0.00	1.38	0.00	45.22	0.00	339.27	46.60	292.66	248.50
3	7.17	35.71	22.57	303.59	91.26	9.79	2.53	0.00	1.69	0.00	52.78	0.00	407.17	54.47	352.70	294.30
5	7.06	38.52	22.65	336.68	89.04	8.61	2.53	0.00	1.38	0.00	59.03	0.00	436.86	60.41	376.45	333.70
6	6.01	8.04	20.34	53.59	14.73	9.92	3.43	0.00	4.23	0.52	19.51	0.00	81.67	24.26	57.41	44.20
7	6.26	10.33	23.51	98.70	26.99	12.14	6.68	2.44	4.26	0.00	13.03	0.00	144.50	17.29	127.21	87.90
8	6.52	7.29	20.24	68.21	19.83	6.83	5.01	1.28	2.71	0.00	12.14	0.00	99.89	14.85	85.04	86.30
9	6.06	7.05	22.72	46.36	12.84	9.92	2.28	0.00	2.71	1.66	13.70	0.00	71.39	18.07	53.32	44.60
10	6.46	8.56	28.19	77.40	25.59	6.83	6.68	0.00	3.86	0.00	9.97	0.00	116.49	13.84	102.65	101.70
11	6.37	6.90	26.97	59.28	19.83	5.05	6.27	0.55	2.43	0.00	9.08	0.00	90.42	11.50	78.92	77.60
12	6.77	4.93	11.80	42.17	14.07	3.87	2.53	0.00	2.91	0.00	7.91	0.00	62.64	10.82	51.82	105.60
13	5.66	6.23	48.59	41.17	12.10	3.26	2.97	0.00	1.41	0.00	2.04	0.00	59.49	3.45	56.04	32.70
15	5.94	8.04	17.72	48.40	12.84	10.18	1.53	0.00	2.62	0.65	20.68	0.00	72.95	23.94	49.01	45.30
16	7.15	37.68	21.41	271.26	80.07	9.18	6.19	0.00	5.22	0.00	21.22	0.00	366.69	26.43	340.26	377.20
18	7.03	29.34	24.58	221.61	54.31	9.35	2.28	1.50	2.23	1.40	41.16	0.00	287.54	44.79	242.75	226.90
20	6.05	9.06	29.66	65.32	14.07	8.31	3.79	0.00	3.19	3.45	15.82	0.00	91.48	22.46	69.02	52.90
21	6.97	34.48	17.65	309.03	55.87	6.74	3.53	0.00	0.82	0.00	119.57	0.00	375.18	120.39	254.78	205.90
22	6.17	16.28	32.35	144.41	24.69	9.35	3.79	1.50	2.91	2.55	33.77	0.00	182.23	39.22	143.01	123.30
23	6.74	34.04	17.85	230.49	44.76	4.13	1.36	0.00	1.13	0.23	98.65	0.00	280.74	100.00	180.74	230.90
24	6.55	27.64	30.05	249.65	51.10	6.74	2.17	0.00	0.93	0.00	24.21	0.00	309.67	25.15	284.52	242.00
26	6.93	39.07	27.91	357.93	94.22	6.09	3.89	0.00	1.47	0.00	47.41	0.00	462.13	48.88	413.25	369.20
51	7.29	42.89	25.72	332.98	66.24	6.35	4.58	0.00	2.12	0.00	57.76	0.00	410.15	59.87	350.28	415.10
52	6.74	9.27	12.12	55.49	14.73	0.74	2.15	0.00	1.18	0.00	14.30	0.00	73.11	15.49	57.62	79.80
55	7.49	49.03	34.58	412.97	42.71	4.13	1.36	0.00	1.41	0.00	31.86	0.00	461.17	33.27	427.90	545.00
56	7.67	60.90	28.31	508.03	83.69	3.83	2.56	0.00	1.41	0.00	36.85	0.00	598.11	38.26	559.84	689.80

[a]All analyses were conducted at the USDA Forest Service Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado. See Wissinger and Whiteman 1992 for additional data for other months and other years.

Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado; also see Wissinger and Whiteman 1992).

Two linear sequences of ponds (51–1–5–18; 52–56–21; see Fig. 31.1) receive runoff that flows over a local outcrop of metamorphosed limestone, and these basins therefore have up to 100-fold greater total dissolved solids and acid neutralizing capacity (ANC) than those that do not receive this runoff (Table 31.2). This local variation in ANC provided the opportunity to isolate the impact of water chemistry on community composition and monitor the potential effects of acidification (Dodson 1982, Harte et al. 1985, Wissinger and Whiteman 1992).

Geomorphology and Hydrology

Many of the basins are embedded in a series of saturated peat fens that have formed in bedrock depressions on the lower shelf of the MCNP. Remote basins are in bedrock (e.g., basins 13, 14, 57) or soil depressions (e.g., basins 55, 15, 19, 20; see Fig. 31.1) formed from slumping and/or snowpack compression (see Windell et al. 1986). Two basins (53, 54) are avalanche impact-ponds with physical and biological characteristics more similar to that of Galena Lake than to the wetlands on the lower shelves (Fig. 31.1).

Climate monitoring stations near our site document that over the past 10 years (1986–96) the area has received an annual average of 130 cm of rain-equivalent precipitation, about 100 cm of which falls as snow (USDA National Resource Conservation Service Snotel Station at Elko Park and NOAA reporting station at RMBL). Total snowfall accumulations range from 1000–1500 cm, with an average maximum snowpack of about 3 m depth. These data probably slightly underestimate the snowfall and snowpack at MCNP, which is 300 m and 600 m higher than Elko Park and RMBL, respectively (A. Meers, B. Barr, personal communication).

Snowmelt is the primary source of hydrological input to all basins and enters mainly as overland flow under the melting snowpack. During peak runoff basins in the main drainages are connected by stream flow and peripheral basins are connected to the largest ponds by overland flow (e.g., 42–1; Fig. 31.1). After snowmelt, the basins within the three main drainages (1–5; 8–5; 12–9) are separated at the surface by saturated fen but retain subsurface connections via the bedrock-confined groundwater in each drainage.

Although there is a gradation in hydroperiods, the basins can be grouped into three hydroperiod categories (Table 31.1). Shallow, hydrologically isolated basins are vernal (sensu Wiggins et al. 1980); they dry by midsummer and usually do not refill until the following spring (Fig. 31.1). Semipermanent, autumnal habitats (after Wiggins et al. 1980) often dry for a short time in late summer but then refill in autumn before ice cover. In two of the past nine years many autumnal basins (51, 52, 55, 6, 4, 6, 8, 10, 11, 15) remained filled throughout the growing season as a result of unusually heavy summer rains (also see Wissinger and Whiteman 1992). Finally, the largest and deepest

basins are permanent ponds that have not dried completely in the past 50 years (1, 3, 5, 9, 12, 18; R. L. Willey, personal communication).

All basins are covered with ice and snow from late October to early summer. Thus, even permanent ponds are filled and free of ice for only about four months, and most temporary basins have a considerably shorter open-water growing season (Table 31.1). During winter the deepest (1–2 m) ponds (1, 5, 9, 12) probably do not freeze solid, although early spring cores suggest that a slushy mixture of water and "frazil ice" (see Oswood et al. 1991) can extend to within 5 cm of the substrate (Whiteman and Wissinger, unpublished data). Freezing in autumnal basins may vary among years. Salamander larvae survive the winter in autumnal ponds when they do not dry (Wissinger and Whiteman 1992), suggesting that either they can survive freezing or there is a thin layer of water similar to that observed in the permanent ponds. However, in most years the nonpermanent basins freeze from the top down to and into the substrate, and therefore are probably most accurately characterized as "aestival" (i.e., liquid water is not available during winter (see Welch 1952, Danks 1971a, Daborn 1974, Daborn and Clifford 1974, Lee 1989, Ward 1992). Freezing appears to be an important source of mortality for aquatic invertebrates in aestival habitats at high latitudes and altitudes (Andrews and Rigler 1985, Daborn 1971, Danks 1971b, Duffy and Liston 1985), and physiological studies suggest that there is considerable variation among species in their tolerance to subfreezing temperatures and physical contact with external ice (Oswood et al. 1991, Frisbee and Lee 1997).

During summer, water temperatures fluctuate considerably on a daily basis, especially in small basins where they can drop at night to 5–10°C and reach daytime highs of 20–30°C (also see Willey 1974). The basins receive relatively high levels of UV radiation as a result of the thin atmosphere, low humidity, and shallow, extremely clear water, and several of the most common zooplankton species in the temporary habitats contain photoprotective carotenoid pigments (see Hairston 1976, 1979).

The various physical habitat characteristics described above can be summarized and compared to other wetlands by evaluating them in the context of Southwood's (1977, 1988) habitat templet, which considers temporal stability (degree of permanence), variability (predictability in drying), and harshness (also see Williams 1987). As in many wetland complexes, the different basins at our study site span the range of temporal stability from vernal to autumnal to permanent. Permanent and vernal basins are the most predictable habitats in that they never or always dry on a seasonal basis, respectively. As in all wetlands, the dry phase of the hydroperiod is a relatively harsh environment for aquatic organisms. However, in high-elevation (and high-latitude [tundra]) wetlands the wet phase of the hydroperiod can also be relatively harsh because of high levels of UV radiation and fluctuating temperatures during the growing season and the frozen, aestival conditions during winter. Because of the year-round harsh conditions, several authors have suggested that the invertebrate fauna of high-elevation wetlands should be impoverished

relative to lower-elevation habitats (Neldner and Pennak 1955, Schmitz 1956, Daborn and Clifford 1974).

Primary Production, Vegetation, and Detrital Inputs

The quillwort, *Isoetes bolanderi,* is the most common submergent plant, and by midsummer this species forms a short (3–10 cm) lawn of vegetation on the soft substrates of many basins. Several ponds (e.g., 10, 11, 56) also contain local patches of starwort (*Calitriche palustris*) and pondweed (*Potamogeton gramineus).* Emergent vegetation is patchily abundant along the edges of the large ponds and throughout the surrounding fens (Fig. 31.1). The dominant shoreline emergents are sedges, rushes, and grasses (*Carex aquatilis, Carex nebraskensis, Juncus confusus,* and *Deschampsia caespitosa*), which are often rooted in a saturated carpet of *Sphagnum* and other mosses (*Polytrichium* sp.) that form floating mats on some pond margins. Thickets of willows (*Salix planifolia*) and other woody vegetation (mainly *Vaccinium caespitosum*) are scattered around the major basins and throughout the peat fens (Fig. 31.1). Emergent species grade landward at the edges of these fens into a diverse transitional plant community dominated by *Carex nova, Caltha leptosepala, Trollius laxus, Pedicularis groenlandica, Sedum rhodanthum, Erigeron peregrinus, Gentian thermalis, Bistorta bistortoides, Swertia perennis, Phleum commutatum, Erythronium grandiflora, Veronica wormskjodlii, Valeriana capitata,* and *Castilleja rhexifolia* (also see Buck 1960). This particular plant assemblage is typical for subalpine fens in this region and has been termed the "*Deschampsia caespitosa/Caltha leptosepala* fen community" (Windell et al. 1996). The surrounding terrestrial habitat on the lower shelf is an open spruce-fir (*Picea engelmanni-Abies lasiocarpa*) woodland that opens into subalpine meadow on the upper shelf. The surrounding terrestrial habitat at MCNP is typical for many of the subalpine wetlands that we have studied at similar elevations throughout the region (see Langenheim 1962).

Benthic substrates are the main site of algal primary production, and a community (30 species identified) dominated by diatoms and desmids (mainly *Frustulia rhomboides, Cymbella lunata, Pinnularia biceps, Cosmarium* spp., and *Staurastrum* spp) is attached to both hard and soft substrates. Qualitative surveys do not suggest major differences in the abundance and taxonomic composition of the periphyton community across basins (Blake, Brown, and Wissinger, unpublished data). Water-column primary production by phytoplankton is extremely low (<50 mg C/m^3 based on chlorophyll-*a* analysis), and the water is therefore extremely clear in all but a few basins with organic staining from peat (e.g., 27–29).

The bedrock and inorganic substrate in most basins is covered with organic sediments that vary from a thin veneer in small isolated basins (e.g., 19, 20, 57) to a thick organic ooze in the centers of the largest ponds (e.g., 1, 5, 12). Peat substrates are common in basins embedded in the fens. Autochthonous inputs are mainly from *Isoetes,* and along pond margins, from patches of

sedges and other emergent vegetation. The latter are of primary importance as a food source for detritivorous aquatic insects that congregate on emergent detritus (Wissinger et al. 1996). Terrestrial organic matter (needles, twigs, branches, leaves) dominates the detritus in basins that are lined with spruce trees (e.g., 8, 14, 15, 19) or willows (e.g., 29, 35, 41, 43).

Salamander Predators

The only aquatic vertebrate in the wetlands at MCNP is the tiger salamander, *Ambystoma tigrinum nebulosum*. Metamorphic (terrestrial) adults of this salamander migrate from terrestrial overwintering sites in late spring and congregate in the largest permanent and semipermanent ponds (1, 3, 5, 6, 8, 9–12), where they mate and deposit eggs. After breeding, metamorphs enter autumnal and vernal basins, where they feed for six to eight weeks before returning to the surrounding forest to overwinter (Whiteman et al. 1994). Eggs typically hatch in mid-July, but, unlike larvae in lower elevation populations, the larvae cannot complete development before the onset of winter and are therefore only likely to survive at this elevation in permanent waters (Wissinger and Whiteman 1992, Whiteman et al. 1994). Metamorphosis occurs after two to five growing seasons, but many individuals forgo it completely and become sexually mature as larvae—i.e., become paedomorphic adults (Whiteman 1994, Whiteman et al. 1996). Paedomorphs and several year-classes of larvae are the top predators in permanent basins at Mexican Cut and other subalpine habitats in the region. In contrast, hatchling larvae and metamorphs are the only salamander stages found in autumnal basins (Table 31.3).

Dietary analyses from stomach pumping indicate that nearly every aquatic invertebrate in these wetlands is consumed by one or more stages of these salamanders (see methods and data in Whiteman et al. 1994; Wissinger and Whiteman, unpublished manuscript). Metamorphs are specialists on fairy shrimp (*Branchinecta coloradensis*), which comprise up to 99 percent of their diet. Larvae exhibit an ontogenetic dietary niche shift in size and in composition, from plankton to benthos. Hatchlings feed mainly on copepods and cladocerans, one-to-two-year-old larvae on larger zooplankton (including fairy shrimp) and small benthic invertebrates (mainly dipteran larvae), and over two-year-old larvae and paedomorphs (together referred to hereafter as "branchiates") on a wide size range of prey, including the largest invertebrate species and smaller salamander larvae. The importance of salamanders as keystone predators on zooplankton has been experimentally demonstrated and undoubtedly underlies patterns of zooplankton distribution and abundance in these wetlands (Dodson 1970, 1974, Sprules 1972). The role of salamander predation in determining benthic community composition is less well understood and has been the focus of much of our experimental work on species interactions.

TABLE 31.3. Distribution and Abundance of Tiger Salamanders at the Mexican Cut Nature Reserve in 1990, Based on Multiple Mark-Recapture Censuses[a]

Pond	Hatchling Larvae	Branchiates	Metamorphs
1	350	1143	2
3	10	61	0
5	0	733	1
6	40	0	4
7	0	0	0
8	450	0	29
9	80	81	4
10	38	0	6
11	40	0	18
12	120	107	8
13	0	0	2
15	0	0	0
18	0	2	0
52	0	0	2

[a]Branchiates are >1-year-old larvae + paedomorphs (see text).

INVERTEBRATE FAUNA

Total Abundance and Biomass

Benthic invertebrate data presented here are based on (1) qualitative surveys from D-net sweeps taken over the past eight years in all basins and (2) replicate quantitative samples using a 0.25-m^2 drop box (see Wissinger 1989) taken on a biweekly basis during the open-water months in 1989–91 in five permanent (1, 3, 5, 9, 12) and six autumnal (6, 8, 10, 11, 55, 56) basins. We avoided taking replicate quantitative samples in the small vernal basins because of the potential for decimating populations in those habitats. Zooplankton samples were taken with an 80 μm mesh net and a 2.2-L Van Dorn sampling bottle mounted on a pole (see Bohonak and Whiteman, manuscript). Biomass estimates from the quantitative data were calculated as the product of number of individuals and taxon-specific individual dry weights (see methods in Whiteman et al. 1996).

Permanent basins have, on average, significantly higher peak densities of invertebrates (3408 $\pm$ 1680 S.D. individuals/m^2) than autumnal basins (1263 $\pm$ 305 S.D. individuals per m^2). However, because the numerically dominant taxa in permanent ponds (cladocerans, copepods, and chironomids) are smaller than those in autumnal ponds (fairy shrimp, caddisfly larvae), the peak standing biomass of autumnal ponds (1864 $\pm$ 630 S.D. mg/m^2) is actually greater than that of permanent ponds (1002 $\pm$ 236 S.D. mg/m^2). Peak abun-

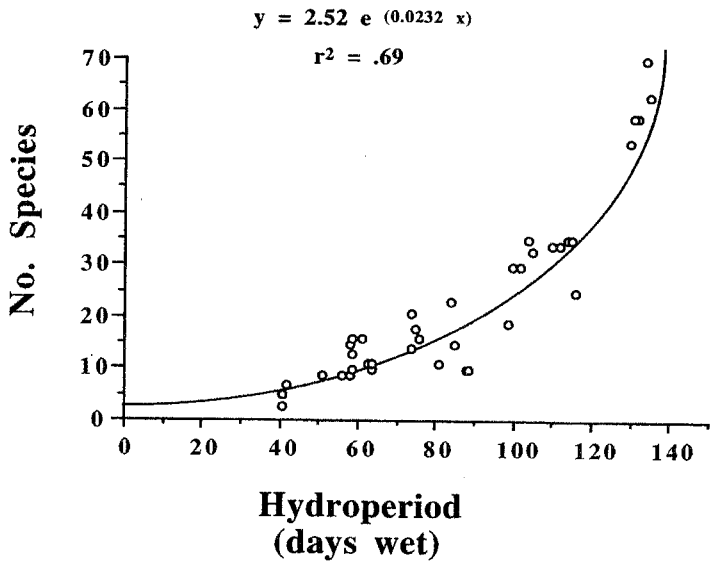
dances in all basins occur in late June to late July, depending on the timing of ice melt in spring. Densities decline in late summer as adults emerge and remain low throughout the fall because many taxa overwinter as eggs that hatch the following spring.

Overall, the invertebrate abundances in these high-elevation wetlands are one to four orders of magnitude lower than is typically reported for low-elevation habitats (e.g., Voigts 1976, Mittlebach 1981, Duffy and Labar 1994, Brinkman and Duffy 1996). Many low-elevation wetlands are eutrophic, with high nitrogen and phosphorus inputs and high autotrophic and/or high detrital production, depending on wetland type (see summary data in Mitsch and Gosselink 1993). In contrast, the subalpine wetlands described in this chapter are, by classical limnological standards, oligotrophic to ultraoligotrophic (see Wetzel 1995). Nitrogen and phosphorus inputs are negligible, autotrophic production is low, and allochthonous detritus are relatively nonnutritious (spruce needles; see Anderson and Cargill 1987). However, based on the few alpine lake studies from western North America that report benthic data (e.g., Taylor and Erman 1980, Donald and Anderson 1980, Hoffman et al. 1996), and on our own surveys of alpine lakes at or near our study site (e.g., Galena Lake, Yule Lakes, Copper Lake, Emerald Lake), the invertebrate communities in the MCNP wetlands appear to be more productive than those in deep lentic habitats at comparable elevations. Most biological limnology of alpine lakes has focused on plankton (e.g., Larson et al. 1996 and references therein), and there is clearly a need for comparative benthic data on production levels and species composition in high-elevation wetlands and lakes.

Community Diversity and Composition

Despite low overall densities, there is a surprising diversity of invertebrates, with approximately 100 taxa identified to date at this single wetland complex (Appendix 31.A). This diversity belies the notion that high-elevation wetlands necessarily have impoverished invertebrate faunas (Schmitz 1956, Daborn and Clifford 1974). Our survey work in other high-elevation wetlands in the vicinity of the RMBL indicates that the diversity at this site is representative for wetlands in the region. Emerging work from other locations in the central Rocky Mountains corroborates our findings that subalpine and montane wetlands are more diverse than previously appreciated (Duffy, this volume, Rader, unpublished data).

Invertebrate diversity at our study site is strongly dependent on hydroperiod (Table 31.2; Fig. 31.2*a*; $F = 1458.5$, $P < 0.001$). This dependence has been observed in other comparative wetland studies (see reviews by Williams 1987, Batzer and Wissinger 1996, and recent papers by Schneider and Frost 1996, Schneider 1997). However, as Schneider and Frost (1996) have noted, interpreting the causal relationships between hydroperiod and diversity can be confounded by other variables, including habitat size. At our study site, basin area and degree of permanence were positively related ($F = 26.5$, $p < 0.001$;



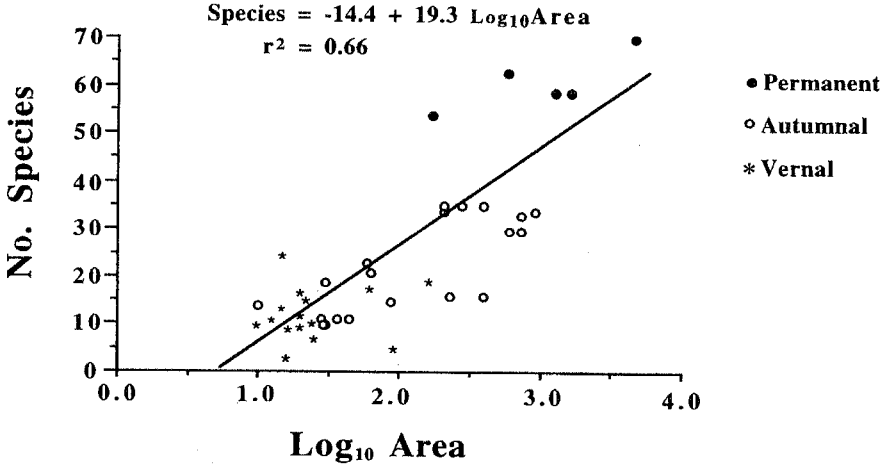


Fig. 31.2. The effects of (*a*) hydroperiod and (*b*) basin area on invertebrate species richness in wetlands at the Mexican Cut Nature Preserve. Data from Table 31.1. See text for statistical analyses.

$r^2 = 0.41$); hence, invertebrate diversity was also strongly associated with basin area ($F = 76.7$, $p < 0.001$; Fig. 31.2b). This species-area effect, while not universally observed (e.g., Ebert and Balko 1987, Schneider and Frost 1996), is well documented for a variety of taxa in freshwater habitats (protozoa, Cairns et al. 1969; zooplankton, Barbour and Brown 1974, Hebert 1986, Dodson 1992; snails, Lassen 1975, Bronmark 1985; beetles, Nilsson 1984; fish, Tonn and Magnuson 1982, Angemeier and Schlosser 1989; and mixed-taxa assemblages, Browne 1981, Roth and Jackson 1987). A second confounding factor is that vertebrate predation is also, as in other wetlands (see Batzer and Wissinger 1996) and lentic habitats in general (see Wellborn et al. 1996), a covariate of permanence. Vertebrate predators (fish or amphibians) are often more abundant in permanent than in temporary basins. Thus, direct effects of habitat drying on diversity are confounded by the effects of predator-mediated coexistence (see reviews by Schneider and Frost 1996, Wellborn et al. 1996).

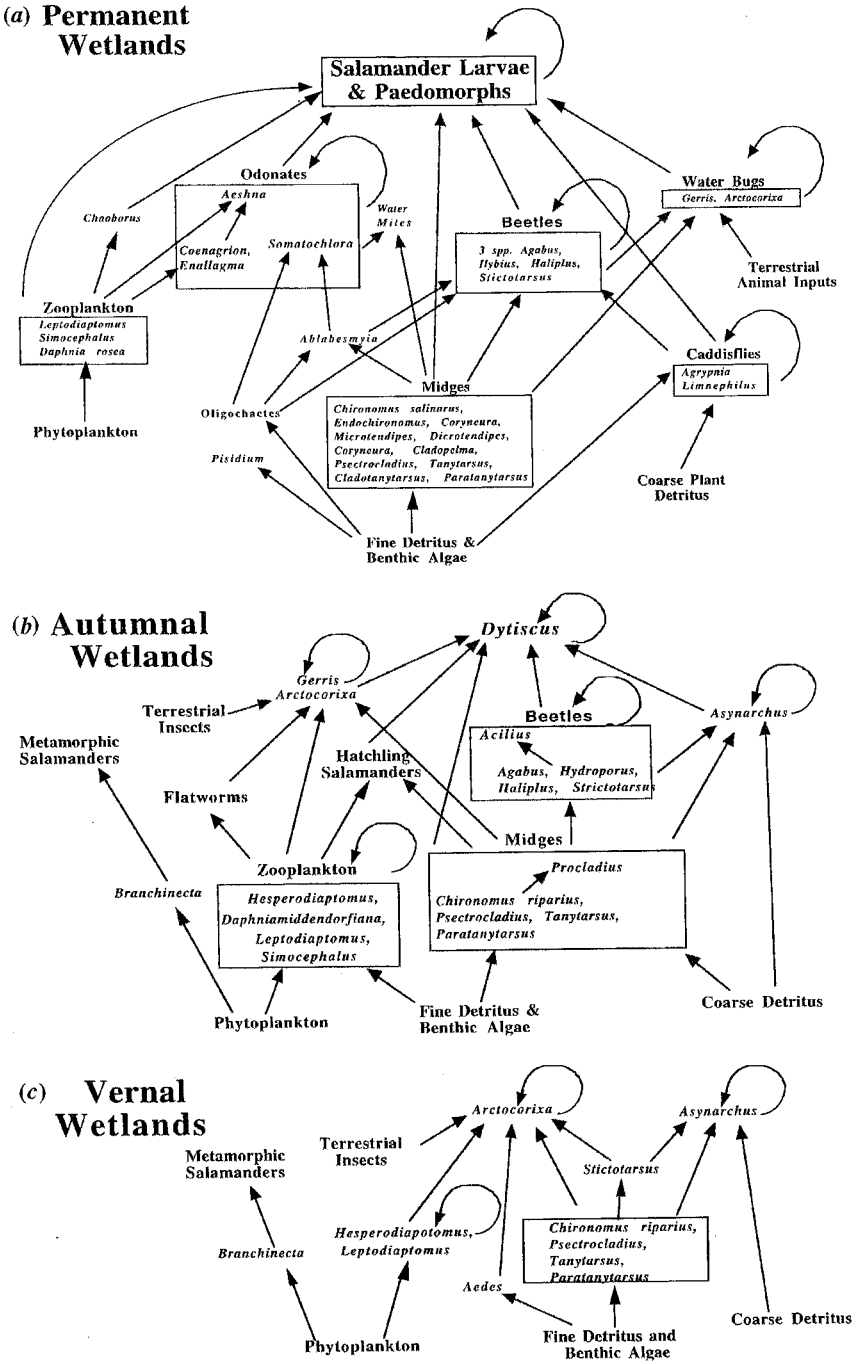
The species composition of the invertebrate assemblage at MCNP is typical for the region (Wissinger and Brown, unpublished data) and, although more diverse, is similar to that reported in small aestival ponds at similar elevations in Colorado and Wyoming (Blake 1945, Neldner and Pennak 1955, Schmitz 1959, Duffy, this volume). Across all habitats, dipterans, particularly chironomid larvae, are the most abundant and species-rich (26 species) group of benthic taxa, followed by beetles (17 species), caddisflies (5 species), water mites (5 species), odonates (5 species), water bugs (5 species), and leeches (3 species) (Appendix 31.A). Cladocerans (7 species), copepods (3 species), and, in temporary habitats, the fairy shrimp *Branchinecta coloradensis* dominate the zooplankton. The dominance of chironomids, and high relative abundances of taxa such as limnephilid caddisflies and dytiscid beetles, appear to be characteristic of high-elevation (see references above) and high-latitude (tundra) wetlands in North America (e.g., Daborn 1974, Butler et al. 1980, Butler 1982). The relatively high proportional abundance of chironomids and other common taxa in alpine and arctic wetlands may reflect their tolerance to freezing conditions during winter (Oswood 1989, Oswood et al. 1991). Alpine and tundra lakes are also dominated by chironomids, but differ from shallow lentic habitats in the relatively high diversity and abundance of mayflies and stoneflies (Taylor and Erman 1980, Donald and Anderson 1980, Andrews and Rigler 1985, Hershey 1985), two groups of taxa that are rare or absent in subalpine wetlands. One exception is the mayfly *Callibaetis ferrugineus,* which, although rare at MCNP, is locally abundant in montane beaver ponds.

Patterns of distribution and abundance among basins are taxon-specific and at least superficially correlated with hydroperiod. In the most diverse groups patterns of distribution and abundance are species-specific, with different taxa restricted or abundant in only one or two of the hydroperiod categories. Among the beetles, only *Strictotarsus* (= *Deronectes*) *grieostriatus* is ubiq-

uitous, with other species restricted mainly to permanent (*Haliplus* spp., *Rhantus gutticollis, Ilybius fraterculus, Agabus strigilosus*) or autumnal habitats (*Acilius semisulcatus, Dytiscus dauricus, Hydroporus* sp., *Hygrotus* sp., *Agabus strigulosus*) (Table 31.1). Among the chironomids several taxa are ubiquitous (e.g., *Paratanytarsus, Psectrocladius, Tanytarsus*), several occur mainly in permanent (e.g., *Chironomus salinaris, Dicrotendipes, Microtendipes, Ablabesmyia*), and several mainly in temporary (vernal + autumnal; e.g., *Chironomus riparius, Procladius*) basins. Zooplankton distribution are similar to those reported at this study site in the 1970s (Dodson 1970, 1974, Sprules 1972). Fairy shrimp (*Branchinecta coloradensis*), the large cladoceran *Daphnia middendorfiana,* and the large copepod *Hesperodiaptomus shoshone* are most abundant in autumnal habitats, whereas smaller species (*Daphnia pulex* and *Daphnia rosea, Chydorus sphaericus*) dominate in permanent habitats. These particular zooplankton assemblages are characteristic of many subalpine ponds near RMBL (R. L. Willey, personal communication) and perhaps across much of the central Rockies (e.g., compare to Duffy, this volume).

In summary, large, permanent basins are most diverse and contain the greatest number of species with restricted distributions (Table 31.1, Fig. 31.3). The primary consumers in permanent-basin foodwebs are dominated by planktonic and epibenthic crustaceans, numerous chironomid midges, and several species of detritus-shredding caddisflies. Dragonflies, beetles, and water bugs are intermediate predators on all of the smaller taxa (zooplankton and chironomids). Several year-classes of larval salamanders (including paedomorphs) are top predators in these basins and are known to prey on nearly all of the dominant invertebrates in the underlying foodweb (Dodson 1970, Dodson and Dodson 1971, Collins and Holomuzki 1984, Holomuzki and Collins 1987, Holomuzki 1989a, b, Zerba and Collins 1992, Whiteman et al. 1994, Whiteman et al. 1996) (Fig. 31.3*a*). In autumnal basins beetle larvae (especially large taxa such as *Dytiscus* and *Acilius*), hemipterans, and caddisflies replace salamander larvae as the top predators on other benthic invertebrates, whereas metamorphic adults and hatchling salamander larvae are the top predators on the large-bodied zooplankton, and occasionally on large benthic taxa such as caddisflies (Fig. 31.3*b*). Finally, vernal foodwebs are the least complex and are dominated by a subset of the fauna found in autumnal basins that can, through a variety of adaptations, complete their life cycles in these extremely ephemeral habitats (Fig. 31.3*c*). These adaptations include:

1. Desiccation-resistant resting stages such as the diapausing eggs of crustaceans (*Leptodiaptomus coloradensis, Daphnia middendorfiana, Acanthocyclops*), rotifers (*Keratella*), mosquitoes (*Aedes communis*), and the adults of the beetles *Strictotarsus grieostriatus* (see reviews of desiccation resistance by Wiggins et al. 1980, Williams 1987, Batzer and Wissinger 1996)


(a) Permanent Wetlands
Salamander Larvae & Paedomorphs
Odonates
Aeshna
Coenagrion, Enallagma
Somatochlora
Chaoborus
Water Mites
Beetles
3 spp. Agabus, Ilybius, Haliplus, Stictotarsus
Water Bugs
Gerris, Arctocorixa
Terrestrial Animal Inputs
Zooplankton
Leptodiaptomus Simocephalus Daphnia rosea
Phytoplankton
Ablabesmyia
Midges
Chironomus salinarus, Endochironomus, Coryneura, Microtendipes, Dicrotendipes, Corynoura, Cladopelma, Psectrocladius, Tanytarsus, Cladotanytarsus, Paratanytarsus
Caddisflies
Agrypnia Limnephilus
Oligochaetes
Pisidium
Coarse Plant Detritus
Fine Detritus & Benthic Algae
(b) Autumnal Wetlands
Dytiscus
Gerris Arctocorixa
Terrestrial Insects
Beetles
Acilius
Agabus, Hydroporus, Haliplus, Strictotarsus
Asynarchus
Metamorphic Salamanders
Hatchling Salamanders
Flatworms
Midges
Procladius
Chironomus riparius, Psectrocladius, Tanytarsus, Paratanytarsus
Zooplankton
Branchinecta
Hesperodiaptomus, Daphniamiddendorfiana, Leptodiaptomus, Simocephalus
Phytoplankton
Fine Detritus & Benthic Algae
Coarse Detritus
(c) Vernal Wetlands
Arctocorixa
Asynarchus
Terrestrial Insects
Metamorphic Salamanders
Stictotarsus
Hesperodiapotomus, Leptodiaptomus
Chironomus riparius, Psectrocladius, Tanytarsus, Paratanytarsus
Branchinecta
Aedes
Coarse Detritus
Phytoplankton
Fine Detritus and Benthic Algae

2. Rapid colonization and development, as in midges (*Chironomus riparius*)
3. Rapid larval development and a diapausing adult stage timed to the dry phase of the hydroperiod, as in caddisflies (e.g., *Asynarchus nigriculus,* Wissinger and Brown, ms.)
4. Seasonal cyclic migrations between adjacent permanent and temporary habitats, as we have observed for *Arctocorixa* water boatmen (Dodson and Dodson 1971)

A Path Analytic Approach to the Problem of Multiple Correlations

As with patterns of diversity, the apparent correlation of particular species and clusters of species with hydroperiod is potentially confounded by other abiotic (water chemistry, area, depth) and biotic (salamander predation) factors that covary with hydroperiod. We used path analysis to further explore the collinear relationships among these habitat variables and to disentangle their direct and indirect effects on community composition. A path analysis is essentially a sequence of multiple regressions structured in a manner that reflects a priori hypotheses about how the variables are related (see general treatments by Tukey 1954, Li 1975, Pedhazur 1982 and ecological applications by Schemske and Horvitz 1988, Edwards and Armbruster 1989, Kingsolver and Schemske 1991, Mitchell 1992, Wooten 1994). We chose this technique over a direct or indirect ordination (e.g., Gower et al. 1994, Larson et al. 1995, Romo et al. 1996, Botts 1997) because we wanted to incorporate biologically relevant information about the habitats into alternative hypotheses

Fig. 31.3. Summary of the dominant taxa and energy pathways in permanent, autumnal, and vernal wetlands at the Mexican Cut Nature Reserve. With a few exceptions, the links are inferred from dietary data that we or others have collected at this particular site. In particular, data for all stages of salamanders are from published and unpublished analyses of stomach contents collected from a nonlethal stomach pumping technique (Wissinger and Whiteman 1992, Whiteman et al. 1994, Whiteman et al. 1996, Wissinger and Whiteman, unpublished ms.). Connections to, from, and within the zooplankton guilds (including *Chaoborus* and flatworms) are based on published data from this site (Dodson 1970, 1974, Sprules 1972, Maly 1973, Maly and Maly 1974, 1980). Caddisfly diets are based on gut dissections (Sparks 1993), midge diets on microscopic examination of gut contents (Wissinger and Brown, unpublished data), odonate diets on fecal pellet analyses (Wissinger, unpublished data), and adult and hemipteran diets on observations of prey capture in natural and experimental (lab and field) settings (also see Reynolds 1975). Inferences about oligochaete and clam diets are based on general literature for these groups and are the least well established for the study site. Loops represent intraguild predation and/or cannibalism within groups and are based on field and laboratory observations (caddisflies, beetles, Hemiptera, salamanders), corroborated in some cases by the dietary data cited above.

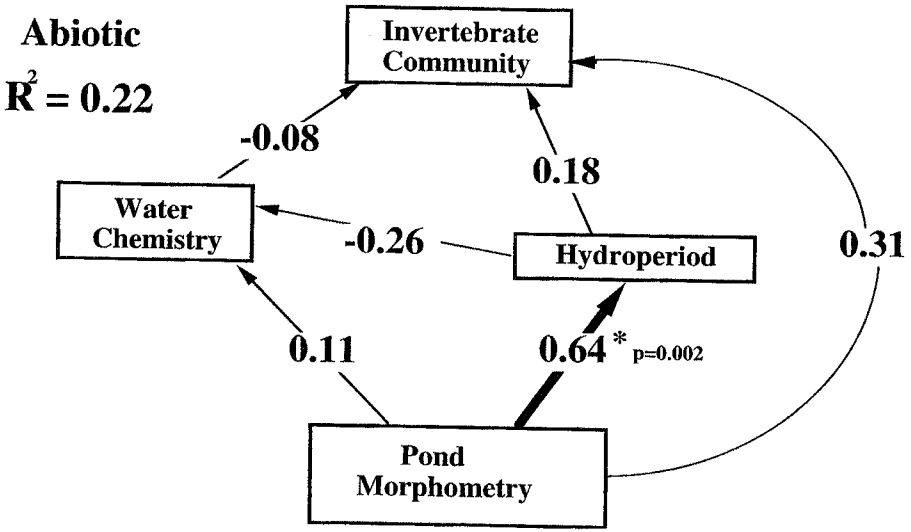
(Edwards and Armbruster 1989). For example, the directionality of cause-and-effect relationships is known and not reciprocal for some pairs of variables (e.g., hydroperiod might affect water chemistry, but not vice versa). A path analysis also can extricate and quantify the relative importance of direct and indirect effects in a nexus of collinear variables (for an example, see Schemske and Horvitz 1988).

The first step was to order the basins according to each of the major factors of interest (most to least permanent, largest to smallest, most to fewest salamander predators, gradients in community composition). For some of the variables this ordering could be accomplished with univariate data. Thus, for hydroperiod we used the average (1989–1996) number of days of ice-free standing water (Table 31.1), and for salamanders we used the separate densities of each life stage (hatchling larvae, metamorphs, large branchiates $\geqq$ one-year-old larvae + paedomorphs; Table 31.3).

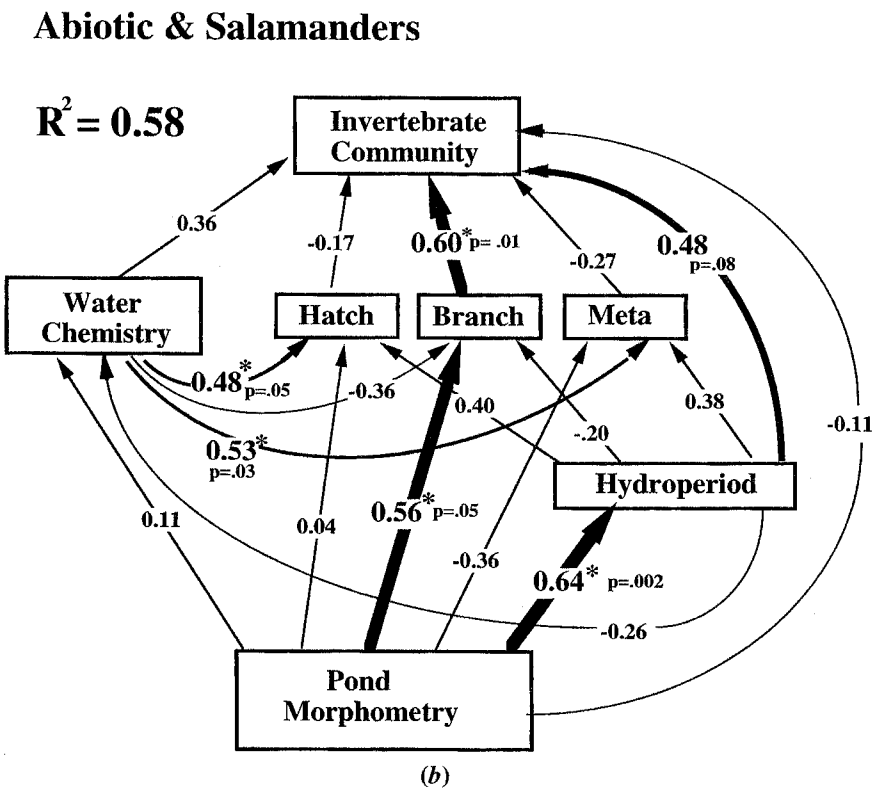
For the other major variables (water chemistry, basin morphometry, and invertebrate community composition) we combined collinear (redundant) measurements into one or a few multivariate dimensions using appropriate ordination techniques. We used principal components analysis (PCA) to combine data on water chemistry (12 variables, see Table 31.2) and basin morphometry (area, depth; Table 31.1). Exploratory analyses (e.g., scatterplots, covariance tests, correlation matrices) indicated that linearity assumptions for PCA were met in both cases. The first PCA axis explained 52 percent and 83 percent of the variance in water chemistry and basin morphometry, respectively. Secondary axes explained little more of the variation for both categories of data and were thus eliminated from the analyses, a broken-stick model being used as a guide (Jackson 1993). The first multivariate axis in the chemistry PCA expressed a gradient from high-alkalinity (relatively high pH, TDS, Ca, Mg, ANC) to low-alkalinity water (relatively low pH, TDS, Ca, Mg, ANC). The primary axis for basin morphometry represented a gradient from large, deep basins to small, shallow basins.

We summarized the invertebrate data in two ways. We first conducted a PCA for the 11 basins for which we had replicate quantitative data and found strong primary and secondary axes. However, our confidence in these axes was compromised by the low number of replicates (11 basins) relative to the large number of species. In order to independently verify the biological relevance of these axes, we also analyzed the presence-absence data from surveys of 41 of the basins (Table 31.1) using multidimensional scaling (MDS), a technique with fewer assumptions than PCA and more appropriate for binary data (see Digby and Kempton 1987). The major axes from the MDS on survey data correlated well with the major axes obtained from the PCA analysis on quantitative data and generally reflected the gradation in taxa observed along the size-hydroperiod-salamander gradient discussed above (Table 31.1, Fig. 31.3).

Having ordered the ponds for all of the variables, we then constructed a series of path analyses in which the overall dependent variable was the first axis from the MDS summary of invertebrate community composition (Fig.



(*a*)



(*b*)

Fig. 31.4. Path analysis diagrams for (*a*) abiotic only effects on invertebrate community composition and (*b*) abiotic + salamander effects on invertebrate community composition. Path coefficients are the partial regression coefficients from multiple regression (see text).

31.4). Path coefficients between each pair of variables were the standardized partial regression coefficients and represent the direct effect of the independent (causal) factor on the dependent (affected) variable for that pair (Pedhazur 1982). We calculated effect coefficients as the sum of direct and indirect path effects (Table 31.4). An explanation for the logic of calculating effect coefficients is given in Schemske and Horvitz (1988). Of the several possible alternative configurations for the abiotic variables, we found that the "best" abiotic model explained only 22 percent of the overall variation in invertebrate community composition (Fig. 31.4*a*). In all of the models,

1. Hydroperiod was directly and significantly ($p = 0.002$) affected by pond morphometry—relatively large, deep basins were more permanent than small, shallow basins.
2. Water chemistry was not related to either basin morphometry or to hydroperiod.
3. Invertebrate community composition was not significantly affected by any of the abiotic variables, including hydroperiod.

We then added salamander predation to the "best" abiotic model and found that this new model explained 58 percent of the variation in invertebrate community composition, more than twice that of analysis with only abiotic effects (Fig. 31.4*b*). In this model the density of branchiate salamanders had the strongest direct effect on invertebrate community composition ($p = 0.01$). Based on the overall effect coefficients (direct + indirect path coefficients), basin morphometry and branchiate salamanders are the two factors that have the greatest overall effect on invertebrate community composition (Table 31.5). The effect of branchiate salamanders is direct, whereas that of basin morphometry is indirect and is translated through its influence on hydroperiod and salamander distributions.

TABLE 31.4. Summary of the Effect Coefficients Calculated from Direct and Indirect Path Effects in Path Analysis with Salamanders[a]

	Direct Effect	Indirect Effect(s)	Effect Coefficient
Pond morphometry	−0.11	0.54	**0.43**
Water chemistry	0.36	−0.53	−0.17
Hydroperiod	**0.48**	−0.29	0.19
Salamanders	−0.17	—	−0.17
Hatchlings			
Metamorphs	−0.27	—	−0.27
Branchiates (larvae paedomorphs)	**0.60**	—	**0.60**

[a] See text and Fig. 31.4.

Mechanisms and the Roles of Life History Studies and Manipulative Experiments

The analysis above suggests that salamander predation is the single most important variable that is directly correlated with patterns of invertebrate community structure. However, we know from life history studies that the distributions of some species are directly due to their inability to complete development in temporary habitats. For example, the caddisfly *Agrypnia deflata,* which occurs only in permanent ponds, emerges in midsummer, mates immediately, and deposits aquatic, desiccation-vulnerable egg masses at a time of the year when only permanent habitats are typically filled (Wissinger and Brown, ms). Similarly, the dragonflies *Aeshna palmata* and *Somatochlora semicircularis* require several years to complete larval development at this elevation, as evidenced by multiple year-classes of larvae (also see Willey 1973). *Somatochlora* larvae can resist short periods of desiccation and are therefore occasionally present in autumnal basins (Willey 1974, Johannsson and Nilsson 1991), but *Aeshna* larvae cannot and are therefore restricted to permanent habitats. Clearly, no additional mechanisms that involve biotic interactions need to be invoked for explaining the distributional patterns of species like *Agrypnia* and *Aeshna.*

However, many of the other taxa with restricted distributions at our study site can complete their life cycles across a range of hydroperiods, and explanations related to species-area relationships and salamander predation are therefore viable alternative hypotheses. Experimental studies implicate salamander predation as the direct or indirect causal factor that underlies patterns of distribution and abundance for two groups of taxa. Field experiments with zooplankton and salamanders at MCNP have demonstrated that the largest species (e.g., *Daphnia middendorfiana, Hesperodiaptomus shoshone,* and *Branchinecta coloradensis*) are dominant competitors over small species and should exclude them in all habitats in the absence of salamander predation (Dodson 1970, 1974, Sprules 1972). However, large species are preferentially preyed on by branchiate salamanders (larvae + paedomorphs) and are therefore eliminated from most permanent ponds, hence allowing small species to flourish (Dodson 1970, 1974; Sprules 1972; Bohonak and Whiteman, ms.).

Field experiments suggest a similar scenario for explaining the distributional patterns of caddisflies. In the absence of salamander predation, a dominant competitor (*Asynarchus nigriculus*) should exclude less aggressive species via intraguild predation (e.g., *Limnephilus externus*). However, preferential predation by salamanders on this dominant competitor indirectly benefits other species which predominate in permanent habitats (Wissinger et al. 1996; Wissinger et al., in press). It is not the large size (as in the zooplankton example) of *Asynarchus* that makes it more vulnerable to salamander predation, but rather its frenetic foraging activities, which appear to be necessary for the timely completion of development in temporary habitats (Wissinger et al. 1999). The tradeoff between high activity levels, which are necessary

for rapid development, and low activity levels, which are necessary for coexistence with vertebrate predators, is an important component of a general conceptual model for shifts in species composition along permanence gradients in lentic habitats (Wellborn et al. 1996). A second tradeoff along this gradient is between prey vulnerability to vertebrate versus large invertebrate predators that replace vertebrates at the top of temporary wetland foodwebs (as in Fig. 31.3). Although numerous examples from the amphibian literature document this tradeoff for amphibian larvae, only McPeek's (1990a, b, 1996) work with *Enallagma* damselflies has demonstrated such a tradeoff for macroinvertebrates.

Given the collinear nature of the effects of basin size, hydroperiod, and shifts in predator effects, attributing patterns of distribution and abundance to any particular mechanism, in the absence of detailed, site-specific life history studies or experimental data can only be speculative. For example, at our study site it is surprising that damselflies occur only in permanent habitats. Closely related species are known to be desiccation and/or freeze tolerant at other locations (Daborn 1971, Sawchyn and Gillot 1974, 1975, Baker and Clifford 1981, Norling 1984), and all three damselflies are abundant in autumnal habitats at lower elevations near our study site (personal observation). Their restriction to permanent habitats at MCNP could be due to (1) the extremely short growing season; (2) the severity of winter conditions in shallow autumnal basins; (3) a species-area effect in which small populations near the limits of their physiological range are likely, at any point in time, to be found only in the largest habitats (also see Jeffries 1994); and/or (4) vulnerability to one or more of the invertebrate predators (e.g., *Dytiscus*) that occur mainly in autumnal habitats at this elevation. Comparative data that might help support or refute these alternatives could be obtained from habitats along a hydroperiod gradient that is comparable in size, or from a series of basins in which hydroperiod and vertebrate predation are completely cross-classified (e.g., permanent but salamander-free habitats). However, few comparative studies are able to cleanly separate alternative hypotheses, and a definitive understanding of the mechanisms that underlie community patterns will be gained most efficiently through replicated field experiments (see review by Wilbur 1997). The well-defined habitat boundaries of subalpine wetlands, their relative simplicity in habitat structure, and their ease of survey and manipulation are all advantages for using them as model systems for understanding the relative importance of biotic and abiotic influences on invertebrate community composition.

ANTHROPOGENIC THREATS AND CONSERVATION

Despite the remote location of many high-elevation wetlands in western North America, these relatively pristine habitats are potentially vulnerable to a variety of human impacts, including mining, deforestation, grazing, water di-

versions, and other activities that occur on both private and public lands, including wilderness areas (see summary by Windell et al. 1986). One regional threat to the western slopes of the Rockies has been the decline in precipitation pH from emissions of coal-fired power plants and cities in the intermountain deserts to the west. Although acid rain in the west is relatively benign compared to that in northeastern North America (Baker et al. 1991, Shannon and Sisterton 1992), many montane habitats are especially vulnerable because of low buffering capacities associated with crystalline bedrock and thin soils (Melack et al. 1982, Kling and Grant 1984, Tonnessen 1984, Harte et al. 1985), and there is some evidence that surface waters in this region are episodically acidified during peak snowmelt in spring (Blanchard et al. 1987, Vertucci and Corn 1996). Wetlands such as those described in this study should be especially vulnerable to pulses of acidity because of their lack of buffering capacity and their small size. In addition to the potential for being directly affected physiologically, invertebrate communities should be affected by any change in the abundance of salamanders, which can be quite vulnerable to acidification (see review by Freda et al. 1991). Harte and Hoffman (1989) hypothesized that a population decline in the salamanders at our study site during the 1980s was related to egg mortality during pulses of acidification in spring. However, since 1988 we have found no evidence that chronic or episodic acidification has had any impact on the salamander population at MCNP (Wissinger and Whiteman 1992; Whiteman and Wissinger, unpublished data). Summer precipitation events during this time period have been circumneutral, and although pH in some years has fallen briefly to below 5.0 during peak runoff in early spring, it has always returned to circumneutral levels by the time salamanders become active and begin to breed (Wissinger and Whitman 1992). There is no evidence to date at this or other study sites in the region to suggest that recent declines in amphibian populations are related to acidification (Vertucci and Corn 1996). Nonetheless, many high-elevation wetlands in the central Rockies remain, by virtue of low buffering capacity, vulnerable to acid inputs and should continue to be closely monitored.

A second threat to the biotic integrity of these habitats is the introduction (via helicopters and fixed-wing aircraft) of trout into high alpine lakes for recreational fishing (e.g., Horton and Ronayne 1996). Many of these lakes and permanent wetlands associated with outflows below these lakes were historically fishless and, like the habitats at MCNP, supported populations of tiger salamanders. It is well known that ambystomatid salamander larvae and paedomorphs are vulnerable to fish predation (Semlitsch 1987, 1988, Jackson and Semlitsch 1993, Figiel and Semlitsch 1990, Sexton et al. 1994 and references therein), and the introduction of trout to these lakes might not only eliminate salamanders but should, based on the results presented in this chapter, lead to changes in invertebrate community composition. In particular, we have hypothesized that permanent habitats with salamanders provide a refuge for invertebrate species that, in the absence of salamanders, would be out-

competed by or preyed on by invertebrates that cannot coexist with salamander predators. Fish introductions have been implicated in community-level changes in high-elevation communities in the northern Cascade Mountains (Liss et al. 1995, Hoffman et al. 1996), but we know of no comparable studies in the central Rockies. Future studies that explore the effects of fish introductions in this region should consider both the direct effects of trout predation on invertebrates and the indirect effects of reducing or eliminating salamanders from the previously fishless habitats.

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APPENDIX 31.A. TAXONOMIC LIST OF MACROINVERTEBRATES AT MEXICAN CUT

Turbellaria
Mesostoma ehrenbergii
Rotifera
Keratella cochlearis
Conochilus hippocrepis
Euchlanis sp.
Oligochaeta
Lumbriculus variegatus
Limnodrilus
Hirudinea
Nephelopsis obscura
Glossiphonia complanata
Helobdella stagnalis
Mollusca
Pisidium
Crustacea
Anostraca
Branchinecta coloradensis
Cladocera
Chydorus sphaericus
Ceriodaphnia quadrangula
Daphnia middendorffiana
Daphnia pulex
Daphnia rosea
Scaphaloberis mucronata
Simocephalus vetulus
Copepoda
Leptodiaptomus coloradensis
Hesperodiaptomus shoshone
Acanthocyclops vernalis
Ostracoda
Cypris palustera
Hydracarina
Arrenurus
Limnesia
Piona
Lebertia
Hydrozetes
Ephemeroptera
Callibaetis ferrugineus hageni
Odonata
Anisoptera
Aeshna palmata
Somatochlora semicircularis
Zygoptera
Enallagma cyathigerum
Coenagrion resolutum
Lestes disjunctus
Hemiptera
Corixidae
Arctocorixa lawsonii
Callicorixa audeni
Coenocorixa bifida
Gerridae
Gerris gillettei
Notonectidae
Notonecta
Trichoptera
Phyrganeidae
Agrypnia deflata
Limnephilidae
Limnephilus picturatus
Limnephilus externus
Asynarchus nigriculus
Hesperophylax occidentalis
Coleoptera
Chyrsomelidae
Plateumaris pusilla
Dytiscidae
Acilius semisulcatus
Agabus tristus
Agabus strigulosus
Agabus kootenai
Dytiscus duricus
Dytiscus alaskanus
Hydroporus
Sanfilippodytes
Ilybius fraterculus
Rhantus gutticolis
Stictotarsus grieostriatus

Haliplidae
Haliplus leechi
Hydrophilidae
Helophorus parasplendidus sperryi
Helophorus eclectus
Hydrobius fuscipes
Gyrinidae
Gyrinus affinis
Staphylinidae
Stenus
Diptera
Ceratopogonidae
Bezzia
Culicoides
Chaoboridae
Chaoborus americanus
Eucorethra underwoodi
Chironomidae
Chironomus salinarius
Chironomus riparius
Cladopelma
Dicrotendipes
Endochironomous
Microtendipes
Pagastiella
Pseudodiamesia
Corynoneura
Cricotopus
Eukiefferella
Paraphaenocladius
Psectrocladius
Ablabesmyia
Procladius
Cladotanytarsus
Paratanytarsus
Tanytarsus
Culicidae
Aedes communis
Aedes pullatus
Tipulidae
Limnophila sp.
Stratiomyidae
Stratiomyia sp.