30 Wetlands of Grand Teton and Yellowstone National Parks

Aquatic Invertebrate Diversity and Community Structure

WALTER G. DUFFY

Aquatic invertebrates were sampled monthly from May through September in six wetlands in Yellowstone and Grand Teton National Parks during 1995. Wetlands sampled exhibited semipermanent, seasonal, and temporary hydrologic regimes. Physical and chemical characteristics of wetland water were similar, except for specific conductance, which was either low ($<60\ \mu S\ cm^{-1}$), *intermediate* (270–$550\ \mu S\ cm^{-1}$), *or high* ($>900\ \mu S\ cm^{-1}$). *A total of 187 taxa of aquatic invertebrates were identified from all samples. Almost 70 percent of the taxa collected had not been reported previously in either park. Taxa richness was greatest in semipermanent wetlands and least in temporary wetlands. Among all wetlands, monthly mean abundance ranged from 18,041* m^{-2}–$335{,}975\ m^{-2}$. *Foodwebs of semipermanent wetlands were most complex, while those in temporary wetlands were most simple.*

GREATER YELLOWSTONE ECOSYSTEM

Yellowstone and Grand Teton National Parks form the core of the Greater Yellowstone Ecosystem (GYE), a 77,000-km^2 area in the north-central Rocky Mountains. Yellowstone National Park was established in 1872 and was the first national park in the world. The park covers 898,349 ha of the northern Rocky Mountains, encompassing a series of high volcanic plateaus and spec-

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tacular river valleys straddling the continental divide. Altitude in the GYE varies considerably and influences local climate since mean annual temperature in the region varies inversely with elevation. Elevation in the central Yellowstone Plateau averages 2377 m and ranges from 1615 m near Gardiner, Montana, at the park's north entrance to 3462 m at Eagle Peak along the southeast boundary (Craighead et al. 1995). Mean annual temperature at Mammoth (2070 m), near the north entrance of the park, is 4°C but is cooler throughout much of the region (Craighead et al. 1995). Precipitation varies from 40–50 cm in the northern range of Yellowstone National Park to 150–175 cm in the northern part of Grand Teton National Park (Farnes 1997). Much of this precipitation is received during late winter snowstorms. Defining features of Grand Teton National Park are the Teton Mountains and Jackson Hole, both the products of a block fault which runs along the base of the Teton Range (Love and Reed 1995). Elevation in Grand Teton National Park ranges from 1981 m at Jackson Hole to 4186 m at Grand Teton Mountain a short distance away. Seven mountain peaks in the Teton Range are above 3658 m (Knight 1994). As in Yellowstone, this spectacular landscape is the product of volcanism, glaciation, and continued geological activity (Love and Reed 1995).

The many palustrine wetlands with temperate thermal regimes in Yellowstone and Grand Teton National Parks have received little attention. Plant communities of wetlands in northern Yellowstone (Chadde et al. 1988), central Yellowstone (Mattson 1984), and parts of Grand Teton (Reed 1952) have been described. The distribution of amphibian species in both parks is relatively well known (Koch and Peterson 1995), and the biology of trumpeter swans (*Cygnus buccinator*) using wetlands in the GYE has been the subject of several investigations (Shea 1981, Tuggle 1986, Squires and Anderson 1995). However, with the exception of species distributions for mosquitoes in Yellowstone National Park (Nielsen and Blackmore 1996) and mollusks in both parks (Beetle 1989), the invertebrate taxa of these wetlands remain largely unknown.

Geothermal wetlands have attracted greater attention (Brock 1967, Brock et al. 1969, Collins 1975, Fraleigh and Wiegert 1975) than those with temperate thermal regimes and, as a consequence, knowledge of their aquatic invertebrate communities is more complete. Source water in these geothermal wetlands ranges from 31–75°C, exhibit extreme variation in pH (2.15 to 8.9) and have high concentrations of Ca (430 ppm), Si (215–400 ppm), and S (120 ppm) (Brock 1967, Collins 1975, Fraleigh and Wiegert 1975). Dense algal mats consisting of one of a few species of blue-green algae develop in these wetlands, reaching maximum biomass (687 mg l^{-1}) at water temperatures of 50–60°C (Brock 1967). Algal biomass is low below 40°C and near the thermal maxima 73–75°C. Two species of brine flies (Diptera: Ephydridae) are common in the thermal wetlands, *Paracoenia turbida* and *Ephydra bruesi* (Brock et al. 1969). Both species colonize and feed on the blue-green algal mat, but neither species colonizes mats where water temperatures are

>41.7°C (Brock et al. 1969, Collins 1977). The brine flies are prey for two water mites, *Partnuniella thermalis* (Acarina: Protsiidae) and *Thermacarus nevadensis* (Acarina: Hydrodromidae), as well as a nonthermophilic fly, *Tachytrechus angustipennis* (Diptera: Dolichopodidae), whose adults feed on the eggs and larvae of Ephydridae near the surface (Collins et al. 1976). Other species colonize these wetlands at water temperatures <30°C (e.g., Diptera: Chironomidae).

The algal-bacterial mat in these thermal wetlands is nutrient-limited and the high biomass of algae persists because most of the mat is in water too hot for Ephydridae to colonize. At water temperatures of 30–40°C feeding by larvae of Ephydridae reduces algal biomass to roughly 50 percent of maximum, algal production is actually greatest in this temperature zone. Through this series of experiments Collins et al. (1976) suggest that feeding by Ephydridae larvae in these systems increases net primary production, increases the efficiency of energy transfer between first and second trophic levels, and affects ecosystem processes (energy transfer) but not prey densities.

In this chapter I present data for nonthermal wetland aquatic invertebrate communities from Yellowstone and Grand Teton National Parks. Data presented are drawn from a longer ongoing study of energy flow in wetlands of the GYE. My objectives are (1) to document the contribution of the wetland aquatic invertebrate community to overall biological diversity in the GYE and (2) to evaluate community composition, diversity, and abundance of wetlands with different hydrologic regimes.

STUDY WETLANDS

Study areas were located in both Yellowstone and Grand Teton National Parks. The study area in Yellowstone is part of the northern range and consists of the lower Lamar River Valley from its confluence with the Yellowstone River, upstream about 6 km to the single bridge over the river. Elevation in the area ranges from about 2400 to 2500 m. Vegetation at lower elevations of the Lamar Valley is sagebrush (*Artemisia* spp.)-grassland steppe, which grades to lodgepole pine (*Pinus contorta* var. *latifolia*) interspersed with grasses (*Poa* spp.) at higher elevations. The area receives heavy use by elk (*Cervus elephus*) and bison (*Bison bison*). Bison graze sedges (*Carex* spp.) in the wet meadow zone of these wetlands during May and September. Elk presumably also use these wetlands, since feces of both are common in their basins.

The primary study area in Grand Teton National Park is located on the Snake River Plain east of Jackson Lake. Surficial geology of this study area is glacial outwash or moraine deposits from the Pinedale, Bull Lake, and older glaciers (Love and Reed 1995) at elevations of 2200–2500 m. Vegetation on the Snake River riparian area consists of an overstory of narrow-leaf cottonwood (*Populus angustifolia*), aspen (*P. tremuloides*), and clumps of blue-spruce (*Picea pungens*) with an understory of willows (*Salix* spp.) and other species. Lodgepole pine predominates on the southern exposure of larger moraines such as Signal Mountain, but is replaced by Engelman spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) on northern exposures. The vegetation colonizing the glacial till outwash area consists of a sagebrush-grassland community. An additional study area was established at the 3200-m elevation in Bridger-Teton National Forest adjacent to Grand Teton. This area is an alpine meadow surrounded by whitebark pine (*Pinus albicaulis*) and Engelman spruce.

Wetlands in the GYE may be classified as riverine, lacustrine, or palustrine (Cowardin et al. 1979). The focus of this chapter is primarily on wetlands that are typically classified as palustrine (i.e., area < 8 ha, water depth < 2 m, lacking wave-formed shoreline features). Larger wetlands (area > 8 ha) may also be classified as palustrine if they are dominated by emergent vegetation, trees, or shrubs. The hydrology of palustrine wetlands is particularly useful for grouping them into similarly functioning units. Cowardin et al. (1979) recognize eight distinct hydrologic regimes. In this chapter aquatic invertebrate data are presented for wetlands having three hydrologic regimes: semipermanently, seasonally, and temporarily flooded. In semipermanently flooded palustrine wetlands, surface water is present during the growing season of most years. Surface water is present for extended periods of the growing season in seasonally flooded palustrine wetlands, particularly early in the growing season. However, surface water is absent by the end of the growing season in most years. In temporarily flooded wetlands surface water is present for only brief periods during the growing season, usually early in the season.

SAMPLING

Aquatic invertebrate samples were collected from six wetlands monthly from June through September 1995, when water was present in basins. However, sampling at wetland SP-sage was not initiated until July, and the temporary wetlands were sampled only during July since they did not contain water on other dates. Aquatic invertebrates were sampled with a 7.6-cm diameter core that was 1.5 m long so that each sample contained surficial sediments and the entire water column. A sliding door with a window of 149-μm nitex was installed 5 cm above the bottom of the core. For collecting a sample, the core was pushed through the water column or an aquatic macrophyte bed until it penetrated the sediment 10–15 cm, the door was closed, and the sample was lifted from the water. The sample was then concentrated either on the nitex door panel or in a 149-μm sieve before being preserved with 90 percent ethanol. Four randomly placed samples were collected from each wetland on each sampling date. Aquatic invertebrates were removed from samples under a stereo microscope at 10× magnification and preserved in 90 percent ethanol until they could be identified. Identification of specimens was to the lowest feasible taxonomic level. Voucher specimens have been prepared and are available by contacting the author.

Foodwebs were constructed using both direct observations of gut contents and information from published literature. The stomachs of ≤10 individuals of common invertebrate predator taxa from each wetland were examined for prey each month. Common invertebrate predators included Odonata, Chaoboridae, predaceous Chironomidae such as *Procladius* spp., and the oligochaete *Cheatogaster* spp. Other invertebrate taxa were assigned to a trophic status from diet information in Merritt and Cummins (1996) or Pennak (1994). Diet of *Ambystoma tigrinum* was inferred from data presented by Sprules (1972) and Holomuzki and Collins (1987).

Physical and chemical data were recorded each time samples were collected. Water temperature was measured with a hand-held thermometer, dissolved oxygen concentration was measured using the Azide modification of the Winkler method, and pH and specific conductance were measured electrometrically. A water sample was collected and frozen for later nutrient analyses. Total phosphorus was measured using the Stannous chloride method and total nitrogen as the sum of ammonia, nitrate, and nitrite nitrogen (APHA 1992).

Density of wetlands in the study areas was determined from 1:24,000 scale draft wetland maps of the area (U.S. Fish and Wildlife Service, Denver, Colorado). Data presented here on wetland density should be considered tentative since only draft maps were available for use.

Cluster analysis was used to group wetlands whose aquatic invertebrate communities were similar. Only the 20 most abundant taxa from each wetland were used in analyses since rare taxa were often associated with a single wetland and confounded results. Statistical analyses were performed with SYSTAT v. 5 software (Wilkinson et al. 1992).

RESULTS

Wetland Distribution

Wetlands exhibiting five and four different hydrologic regimes were identified in the Yellowstone and Grand Teton study areas, respectively (Table 30.1). Seasonally flooded wetlands were the most common type of wetland in both study areas, particularly at higher elevations. Semipermanent wetlands were found only at low and middle elevations. Saturated wetlands were distributed throughout the Lamar Valley but were not found in the Grand Teton study area. Few temporary and permanent wetlands were found in either study area.

Water Chemistry and Basin Morphometry

Water in the wetlands sampled was similar physically and chemically, except for specific conductance and maximum depth. Three ranges of specific con-

TABLE 30.1. Density (no. km^{-2}) of Palustrine Wetlands within Three Elevation Zones in the Study Areas of Yellowstone and Grand Teton National Parks

	Yellowstone			Grand Teton		
Wetland Class	<2500 m	2500–2700 m	>2700 m	<2500 m	2500–2700 m	>2700[a] m
Saturated	0.8	0.4	0.4	0	0	0
Temporary	0.1	0	0	0.1	0	0
Seasonal	2.3	1.8	4.4	2.8	1.8	5.0
Semipermanent	0.3	0.9	0	1.7	0.5	0
Permanent	0.1	0	0	0	0	6.0
All classes	3.6	3.1	4.8	4.6	2.3	11.0
Area sampled	49.0	29.0	2.5	13.5	8.0	2.0

[a] Represents density of wetlands above 2700 m elevation in a meadow of the Teton Range, not the entire region.

ductance were observed. Low-conductance water ($\leq 60\ \mu S\ cm^{-1}$) was found in the SP-spruce wetland and the T-meadow1 and T-meadow2 wetlands (Table 30.2). Intermediate-conductance (270–$550\ \mu S\ cm^{-1}$) water was found in the SP-sage wetland and the S-fir wetland. Relatively high-conductance ($930\ \mu S\ cm^{-1}$) water was found in the T-aspen wetland. Maximum depth of the wetlands sampled was consistent with their hydrologic classification. Semipermanent wetlands retained water throughout the period, the seasonal wetland became dry between August and September, and the temporary wetlands contained water only from late June through early July. pH of water in most wetlands was neutral or slightly basic. However, pH of SP-fir ranged from 6.3 to 6.9 S.U. Other chemical and physical characteristics varied little among wetlands (Table 30.2). Total nitrogen concentration exceeded $1.0\ mg\ l^{-1}$ in all wetlands sampled, and total phosphorus concentration ranged from 0.01–$0.05\ mg\ l^{-1}$.

Invertebrate Community Composition and Diversity

A total of 187 taxa representing 24 orders of aquatic invertebrates were collected from the six wetlands sampled during 1995 (Appendix 30.A). This included 43 taxa (genera or species) of flies, making Diptera the most diverse order collected. In addition to Diptera, 25 species of water fleas (Cladocera), 21 species or genera of beetles (Coleoptera), 14 species of worms (Tubificida), and 11 species of snails (Gastropoda) were found. Almost 70 percent (129) of the 187 taxa collected had not been previously recorded from either park.

Number of taxa recorded in wetlands ranged from 2 in the T-aspen wetland to 98 in the SP-spruce wetland (Table 30.3). Most taxa were collected with quantitative methods. However, as many as 18 taxa not recorded in quantitative samples were collected with qualitative methods. Taxa richness, as mean per sample, mean per month, and total, was greater in semipermanent and seasonal wetlands than in temporary wetlands.

Cluster analysis using all 187 taxa suggested patterns of aquatic invertebrate community composition among types of wetlands (Fig. 30.1). Communities in the 2 T-meadow wetlands sorted distinctly from those in other wetlands. The community in the SP-sage wetland located in the Lamar Valley also differed from the other wetlands. K-means clustering using the 20 most abundant taxa in each wetland suggested the two semipermanent wetlands (SP-sage, $F = 160.10$, and SP-spruce, $F = 197.01$) were similar and differed from the S-fir ($F = 57.16$) and both T-meadow wetlands ($F = 0.18$). Two or three taxa were associated with three of the clusters. High densities of two midge larvae, *Cladopelma* spp. and *Paratanytarsus* spp., were uniquely associated with the SP-sage wetland. Similarly, high densities of two seed shrimp (Ostracoda), *Cypridopsis vidua* and *Cypris palustra*, distinguished the invertebrate community of the SP-spruce wetland from other wetlands. A third cluster consisted of two water fleas (*Simocephalus serrulatus* and *Chydorus sphaericus*) and immature cyclopoid copepods that were common in SP-sage,

TABLE 30.2. Water Quality Parameters Measured at Six Wetlands in Yellowstone and Grand Teton National Parks during 1995[a]

	Abbreviated Wetland Name				
Parameter	SP-sage	SP-spruce	S-fir	T-meadow	T-aspen
Hydrologic regime	Semipermanent	Semipermanent	Seasonal	Temporary	Temporary
Vegetation zone	Big sagebrush	Engelmann spruce	Subalpine fir	Subalpine meadow	Aspen
n	1	1	1	2	1
Water depth (cm)	50–104	100–166	0–65	0–30	0–20
Water temperature (°C)	13.0–22.0	8.5–19.0	10.8–15.2	19–21.5	27.5
Dissolved oxygen (mg × l^{-1})	2.6–5.5	1.2–3.4	1.6–4.5	—	—
pH (S.U.)	8.2–10.0	6.3–6.9	7.2–8.5	7.5–8.5	9.2
Conductance (μS × cm^{-1})	450–550	10–20	270–390	50–60	930
Maximum depth (cm)	50–104	100–166	0–65	0–30	0–20
Total nitrogen	1.21–1.44	0.94–1.34	1.31	—	—
Total phosphorus	0.01–0.05	0.01–0.05	0.01	—	—

[a] Data are ranges recorded during the sampling.

TABLE 30.3. Mean and Total Taxa Richness at Six Wetlands in Yellowstone and Grand Teton National Parks during 1995[a]

	Abbreviated wetland name				
Parameter	SP-sage	SP-spruce	S-fir	T-meadow (1 and 2)	T-aspen
Mean richness · sample^{-1}	22.7 (4.6)	18.8 (4.3)	19.2 (4.9)	10.8 (2.5)	2 (0.0)
Mean richness · month^{-1}	35.7 (0.6)	34.0 (2.2)	39.3 (5.0)	21 (—)	2 (—)
Total richness · wetland^{-1}	63	98	92	21	2

[a] Numbers in parentheses are standard deviations.

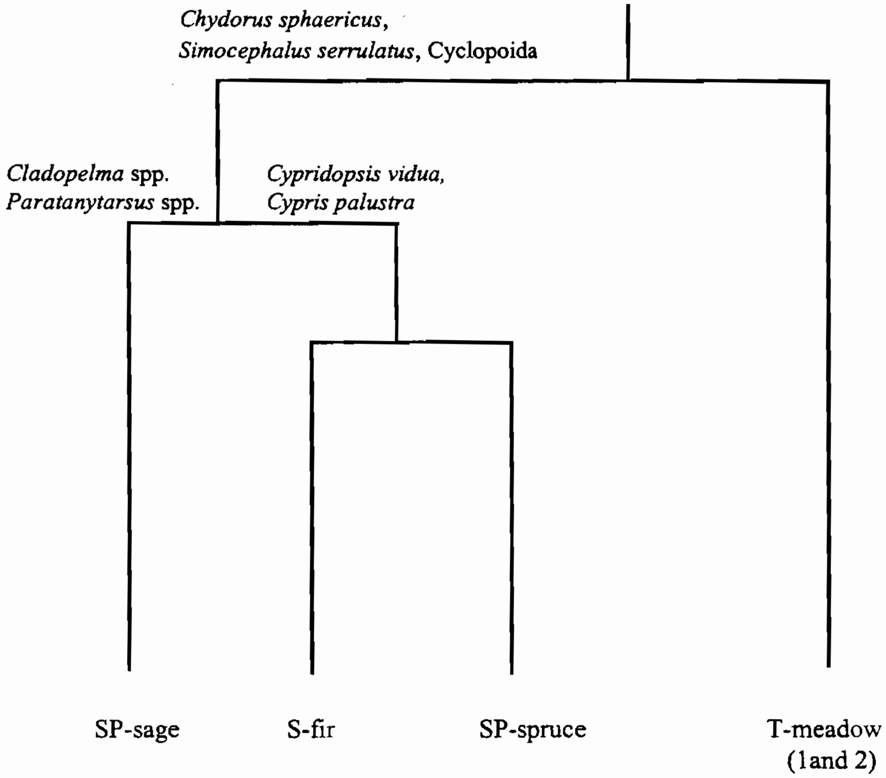

Fig. 30.1. Dendogram illustrating results of cluster analysis of aquatic invertebrate community composition and mean abundance in four types of wetlands in Yellowstone and Grand Teton National Parks.

SP-spruce, and S-fir, but absent from or uncommon in the T-meadow wetlands (Tables 30.4–7).

Invertebrate Abundance

Abundance of aquatic invertebrates was greatest in the SP-sage wetland in the Lamar River Valley and least in the T-meadow wetlands. Abundance in the SP-sage wetland ranged from about 68,000 organisms · m^{-2} in July to almost 336,000 organisms · m^{-2} in August (Table 30.4). Benthic organisms comprised more than 65 percent of the invertebrates collected from this wetland, with midge larvae being particularly abundant. In contrast, 90 percent

TABLE 30.4. Seasonal Abundance (no. m^{-2}) of Aquatic Invertebrates in Wetland SP-sage in the Lamar River Valley, Yellowstone National Park during 1995

Taxon	July	August	September
Annelida			
Cheatogaster diaphanus	2,806	1,751	907
Limnodrilus udekemianus	1,751	4,009	696
Other Annelida	3,017	528	1,688
Cladocera			
Ceriodaphnia reticulata	63	17,787	3,165
Daphnia pulex	7,069	1,372	317
Simocephalus serrulatus	1,118	13,399	20,108
Chydorus sphaericus	422	11,500	17,260
Other Cladocera	22,282	38,824	5,064
Copepoda			
Macrocyclops albidis	0	1,118	3,904
Eucyclops agilis	10,023	2,743	2,743
Aglaodiaptomus forbesi	0	1,329	63
A. leptopus	802	3,904	1,857
Other Copepoda	211	7,026	7,619
Ostracoda			
Cypridopsis vidue	2,638	1,372	63
Cypris palustra	3,545	5,549	1,751
Other Ostracoda	0	0	63
Insecta			
Cladopelma sp.	1,013	4,431	146,814
Paratanytarsus sp.	5,127	163,483	10,339
Procladius sp.	1,435	28,865	30,068
Psectrocladius sp.	0	10,656	1,646
Other Insecta	2,110	13,989	6,204
Mollusca			
Sphaerium nitidum	1,435	4,811	3,376
Other Mollusca	1,582	63	0
Total	67,794	335,975	267,337

TABLE 30.5. Seasonal Abundance (no. m^{-2}) of Aquatic Invertebrates in Wetland SP-spruce on Signal Mountain, Grand Teton National Park during 1995

Taxon	June	July	August	September
Annelida				
Cheatogaster diaphanus	274	3,650	0	0
Ophidonais serpentina	633	0	2,638	2,532
Other Annelida	169	63	654	506
Cladocera				
Ceriodaphnia reticulata	0	1,013	0	0
Simocephalus serrulatus	4,748	1,857	7,258	6,035
Chydorus sphaericus	696	18,948	10,086	11,056
Other Cladocera	2,827	8,335	6,056	4,368
Copepoda				
Acanthocyclops vernalis	211	0	106	127
Macrocyclops albidis	0	106	2,743	2,891
Aglaodiaptomus forbesi	169	63	928	886
Harpactaoida	2,743	9,136	971	612
Other Copepoda	7,069	4,959	5,043	4,368
Ostracoda				
Cypridopsis vidue	5,170	10,930	55,788	43,951
Cypris palustra	0	118,223	35,575	40,660
Other Ostracoda	2,595	1,076	8,524	9,263
Insecta				
Microspectra sp.	0	380	823	928
Procladius sp.	0	591	169	190
Psectrocladius sp.	0	422	5,402	6056
Chaoborus americanus	169	105	528	506
Other Insecta	485	1,097	3,165	2,638
Total	31,439	184,625	150,654	141,581

of the organisms collected from the SP-spruce wetland were water-column invertebrates (Cladocera, Copepoda, and Ostracoda), and midge larvae were uncommon (Table 30.5). Predators, primarily dragonfly and phantom midge larvae (Odonata and *Chaoborus americanus*), were regularly collected in low numbers from the SP-spruce wetland.

Abundance in the S-fir wetland reached more than 143,000 organisms · m^{-2} in August, before the wetland dried out. Water fleas were the most common organisms collected from this seasonal wetland, particularly *Simocephalus serrulatus* and *Chydorus sphaericus* (Table 30.6). Two species of aquatic worms (Oligochaeta) were abundant in June, while another predatory worm (*Chaetogaster diaphanus*) was abundant in August. Midge larvae were most abundant in this seasonal wetland during August.

Aquatic invertebrate abundance was lower in the temporary wetlands than in other wetlands sampled. Mean abundance in the T-meadow1 and T-meadow2 wetlands was about 18,000 organisms · m^{-2} (Table 30.7). Midge

TABLE 30.6. Seasonal Abundance (no. m^{-2}) of Aquatic Invertebrates in a Seasonal Wetland S-fir in Grand Teton National Park during 1995

Taxon	June	July	August
Annelida			
Cheatogaster diaphanus	0	63	11,352
Ophidonais serpentina	528	0	0
Paranais littoralis	7,912	0	0
Limnodrilus udekemianus	6,921	0	0
Other Annelida	5,824	950	63
Cladocera			
Ceriodaphnia reticulata	1,118	1,794	9,875
Simocephalus serrulatus	1,161	7,343	16,247
Chydorus sphaericus	106	211	54,818
Other Cladocera	5,612	1,794	10,445
Copepoda			
Acanthocyclops vernalis	0	169	1,224
Harpactaoida	7,913	63	0
Other Copepoda	22,113	7,448	14,728
Ostracoda			
Cypridopsis vidue	950	739	2,954
Cypris palustra	422	2,701	0
Other Ostracoda	29,561	5,781	63
Crustacea			
Lynceus brachyurus	633	63	0
Insecta			
Heterotrissocladius spp.	0	0	6,710
Microspectra spp.	1,899	0	4,853
Procladius spp.	0	274	844
Psectrocladius spp.	1,561	5,191	5,528
Other Insecta	2,743	7,385	6,773
Mollusca			
Sphaerium securis	380	591	317
Other Mollusca	105	421	211
Total	104,234	40,934	143,480

larvae (*Psectrocladius* spp.) and a calanoid copepod (*Hesperodiaptomus shoshone*) were the most abundant taxa in these temporary wetlands. Abundance was greater in the T-aspen wetland, but only two taxa occurred in this wetland (Table 30.7).

Aquatic Foodwebs

Foodweb complexity was greatest in the two semipermanent wetlands and most simple in the temporary alpine meadow wetlands (Fig. 30.2). Although the T-aspen wetland contained only two taxa, it was considered somewhat of

TABLE 30.7. Mean Abundance (no. m^{-2}) of Aquatic Invertebrates in Subalpine Temporary Wetlands T-meadow in Shoshone National Forest and T-aspen in Grand Teton National Park during July 1996

Taxon	T-meadow1 and T-meadow2	T-aspen
Cladocera		
Daphnia pulex	106	47,475
D. schodleri	106	0
Other Cladocera	0	0
Copepoda		
Acanthocyclops vernalis	106	0
Hesperodiaptomus shoshone	3,376	0
Leptodiaptomus coloradensis	950	0
Other Copepoda	633	0
Ostracoda		
Candona spp.	1,372	0
Cypridopsis vidue	1,266	12,660
Other Ostracoda	0	0
Crustacea		
Brachinecta coloradensis	422	0
Insecta		
Aedes cataphylla	528	0
A. fitchii	317	0
Psectrocladius spp.	6,753	0
Other Insecta	106	0
Total	16,041	60,135

an anomaly. Top predators in the SP-sage wetland were tiger salamander (*Ambystoma tigrinum*) larvae. Tiger salamander larvae were not found in the SP-spruce wetland, where an intermediate predator guild included damselfly, dragonfly, and predaceous diving beetle larvae as well as true aquatic bugs (Hemiptera). Prey consumed by the odonate predators included midge larvae, other insects, seed shrimp, Cladocera, and copepods of varying sizes. Although I did not determine the diets of predaceous diving beetles and true aquatic bugs (Notonectidae, Gerridae), their diets are reported to be similar to those of most odonates (Holomuzki 1985, Merritt and Cummins 1996). A third predator guild was represented by predaceous genera of midge larvae and aquatic worms. Stomachs of these taxa often included small species of water fleas, immature copepods, or early-instars of midge larvae. Phantom midge larvae represented a fourth predator guild in the semipermanent wetlands, but occurred only in the SP-spruce wetland. Prey of phantom midges included nekton ranging in size from larger seed shrimp to small water fleas such as *Chydorus sphaericus*. Two taxa, the fingernail clam *Sphaerium nitidum* and the aquatic worm *Limnodrilus udekemianus,* coexisted with these aquatic predators. The foodweb of the seasonal wetland S-fir was similar to

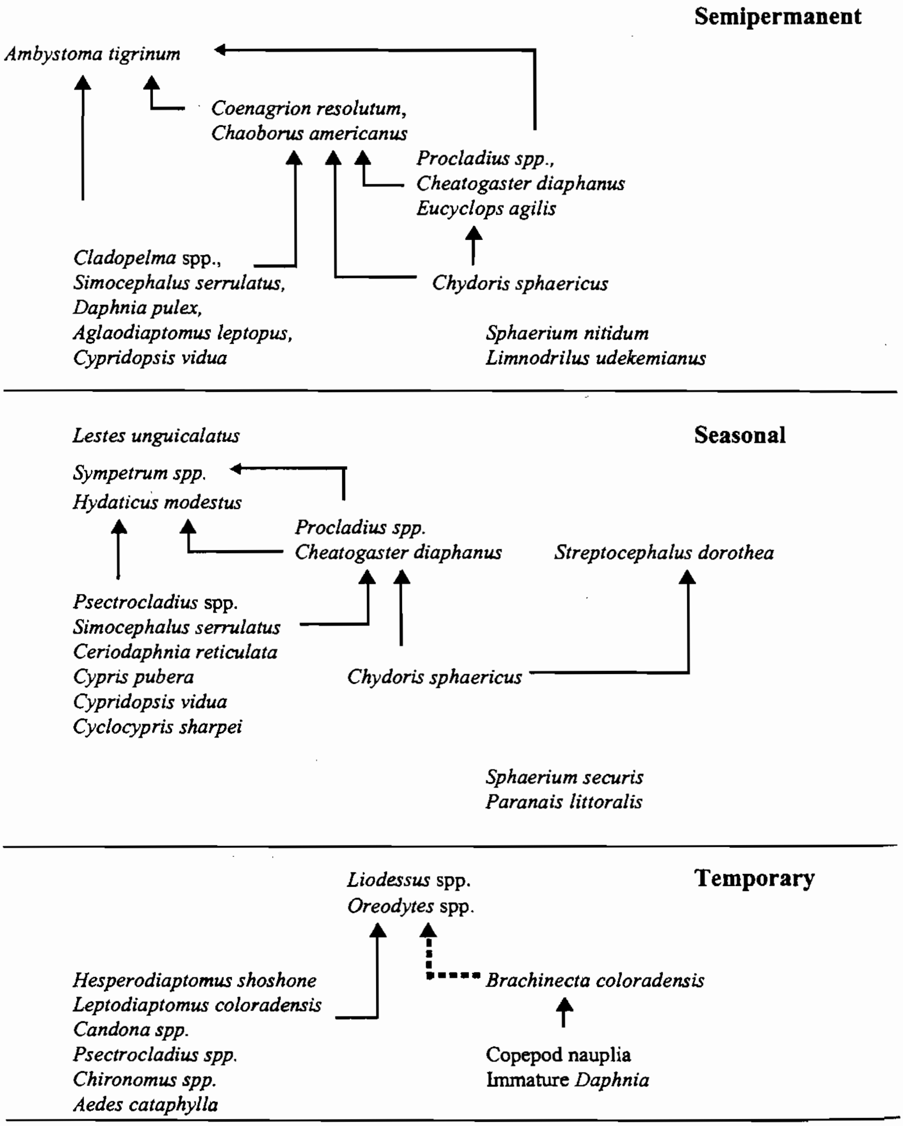

Fig. 30.2. Generalized foodweb for semipermanent (top panel), seasonal (middle panel), and temporary subalpine wetlands (bottom panel) in the GYE.

the foodweb of semipermanent wetlands, but lacked a vertebrate predator. Filter-feeding fairy shrimp (*Streptocephalus dorothea*) capable of ingesting smaller zooplankton also appeared in seasonal wetlands. Top predators in the foodweb of the temporary (T-meadow) wetlands were two genera of predaceous diving beetles (Dytiscidae) (Fig. 30.2). A fairy shrimp capable of ingesting smaller zooplankton was also found in the T-meadow wetlands, with the remainder of the community consisting of filter-feeding copepods, water fleas, mosquito larvae, and collector-gatherer midge larvae.

DISCUSSION

Taxonomic Composition and Diversity

The aquatic invertebrate communities of wetlands in Yellowstone and Grand Teton National Parks were found to be quite diverse, with a total of 187 taxa recorded from only one year of sampling. The diversity of aquatic invertebrates in these wetlands should not be surprising, since they provide habitats that are structurally complex, productive and of varying hydroperiod and have water that varies in concentrations of dissolved constituents. Life history strategies employed by 148 aquatic invertebrate genera to colonize wetlands in eastern North America have been categorized by Wiggins et al. (1980). However, the difficulty of sampling aquatic invertebrates in wetlands and extracting animals from organic detritus has hampered developments in this field. Consequently, the contribution of wetland aquatic invertebrate communities to ecosystem biodiversity is often overlooked, even by specialists. For example, Reice (1994) characterizes aquatic macroinvertebrate communities in "ponds" worldwide as being impoverished of species. While fewer taxa are typically found in wetlands than in clean running waters, wetlands are capable of supporting diverse aquatic invertebrate communities.

Where entire wetland aquatic invertebrate communities have been studied, they have typically been diverse. In Australia 137 taxa were recorded from 33 wetlands during one year (Growns et al. 1992), while sampling a similar number of wetlands (29) during early summer in Scotland produced 125 taxa (Jeffries 1994). In North America Olson et al. (1995) record 93 aquatic macroinvertebrate taxa from a northern prairie wetland. Studies of wetlands bordering a Great Lakes connecting river also documented a diverse aquatic invertebrate community having 171 taxa (Duffy et al. 1987). Forty-eight taxa were found in a southern bottomland forest that retained water only during the winter and early spring (Duffy and Labar 1992). Together, these data suggest that wetlands in regions around the globe may support aquatic invertebrate communities composed of from 100–200 taxa during seasons favorable for growth and development.

Taxonomic composition of wetland aquatic invertebrate communities in Yellowstone and Grand Teton National Parks differed among wetlands of varying hydroperiod. Diversity was generally greater in wetlands having longer hydroperiods. Predominant taxa in the SP-sage and SP-spruce, two semipermanent wetlands, also differed. The SP-sage wetland in the Lamar River Valley was characterized by high densities of two genera of midge larvae, *Cladopelma* and *Paratanytarsus*. In contrast, midge larvae were not abundant in the SP-spruce wetland, which was characterized taxonomically by two species of seed shrimp, *Cypris palustra* and *Cypridopsis vidua*. Three of these four taxa are recognized as associated with more permanent water (Wiggins et al. 1980, Bazzanti 1997). The presence of tiger salamander larvae in the SP-sage wetland may be responsible for observed differences in community composition between these two wetlands. The prey of tiger salamanders varies with ontogeny (Leff and Bachmann 1986), with small larvae consuming primarily small crustacean zooplankton, then incorporating larger invertebrates or prey such as small fish into their diet as they grow (Leff and Bachmann 1986, Holomuzki and Collins 1987). Sprules (1972) demonstrated that tiger salamanders are capable of restructuring the foodwebs in subalpine wetlands. Primary predators in the SP-spruce wetland were invertebrates (larvae of phantom midges, dragonflies, predaceous diving beetles) that are considered incapable of regulating prey populations (Johnson and Crowley 1980). Other factors possibly contributing to differences in invertebrate community composition between these semipermanent wetlands include surrounding vegetation type and water chemistry. The SP-spruce wetland has a small drainage basin within a Englemann spruce/lodgepole pine forest. These factors likely contribute to the low concentrations of dissolved salts and low pH in the water from this wetland, compared with other wetlands.

The seasonal wetland in the subalpine fir zone (S-fir) was characterized as taxonomically similar to the SP-spruce wetland, with high densities of seed shrimp. Similarities in the communities of these two wetlands may have also been influenced by surrounding upland vegetation and small drainage basin. This seasonal wetland was also located within 200 m of a semipermanent wetland, and migration of some taxa could be expected. In addition to the seed shrimp, predominant taxa in this seasonal wetland during spring included immature cyclopoid copepods, aquatic worms (*Paranais littoralis*), and a fairy shrimp (*Streptocephalus dorothea*). The aquatic worms were found almost exclusively mining the stems of dead emergent vegetation. Several genera of midges associated either with seasonal hydroperiods (*Psectrocladius*) or clean water (*Hetertrissocladius*) became common in late summer (Beck 1977, Bazzanti et al. 1997).

The invertebrate community found in the temporary alpine meadow wetlands (T-meadow1 and T-meadow2) was characterized by the lack of *Simocephalus serrulatus, Chydorus sphearicus,* and cyclopoid copepodids. All three of these taxa were considered overwintering residents by Wiggins et al. (1980). Lack of copepods has also been reported as characteristic of some aquatic invertebrate communities in temporary Australian wetlands (Growns et al. 1992). Predominant species in these temporary wetlands were large fairy shrimp (*Brachinecta coloradensis*) and the calanoid copepod *Hesperodiaptomus shoshone,* a species that is restricted to elevations of >3000 m (Pennak 1994). Larvae of two genera (*Laccodytes* and *Oreodytes*) of predaceous diving beetles also inhabited these wetlands, and individuals collected with a dip net were 80–100 mm long. The presence of these rather large predators was surprising since temporary wetlands often lack predators or have very few (Schneider and Frost 1996).

Only two species were found in the T-aspen temporary wetland. However, these wetlands were used as mineral licks by moose (*Alces alces*). Moose visited these wetlands daily, and their activities had denuded vegetation from the wetland and surrounding area, leaving the water extremely turbid.

Invertebrate Abundance

Abundance of aquatic invertebrates in wetlands from Yellowstone and Grand Teton National Parks was considered to be generally high. However, comparisons with published information from other regions are made difficult by the variety of approaches taken and sampling methods employed. For example, in prairie wetlands Duffy and Birkelo (1997) report aquatic macroinvertebrate densities from core samples ranging from 4700–20,000 · m^{-2}, while Neckles et al. (1990) report densities of total aquatic invertebrates from activity traps of up to 210,000 · m^{-2}. Densities reported from Great Lakes coastal wetlands also vary. Density of all aquatic macroinvertebrates in Gerking samples from wetlands along the St. Mary's River flowing from Lake Superior ranged from 7000–20,000 · m^{-2} (Duffy et al. 1987). Using a core sampler, Botts (1997) found that density of midge larvae in ponds along the Lake Erie shore ranged from about 5000 to > 200,000 · m^{-2}. The upper range in abundance from these and the present study suggests that density of aquatic invertebrates in wetlands may frequently approach or exceed 100,000–200,000 · m^{-2}. Sampling both water-column and benthic habitats and using fine mesh sieves, as was done in this study and by Botts (1997), presents difficulties. However, more quantitative methods should be encouraged, since they will reveal the true diversity and abundance of aquatic invertebrate communities in wetlands.

The abundance, distribution, and diversity of aquatic invertebrate communities reported here seems consistent with the growing body of literature for wetlands worldwide. However, the interpretations were based on data from the initial year of a long-term study, and limited replication precluded the application of more rigorous statistical procedures.

Invertebrate Diversity and Ecosystem Function

The role of wetlands and the aquatic invertebrates inhabiting them in the processes or functioning of the Greater Yellowstone Ecosystem remains largely unknown. Wetland aquatic invertebrate communities are generally recognized for their role in food chain support. They are the primary link between primary production/detrital resources and vertebrates. Birds such as waterfowl require a diet high in protein during specific life stages and may feed exclusively on aquatic invertebrates to meet these demands (Swanson and Duebbert 1989). Other wetland-associated birds, such as red- and yellowheaded blackbirds, marsh wrens, and shorebirds, also consume aquatic invertebrates (Weller 1994). Fish may occur naturally in some wetlands, but are usually absent from those having irregular hydrologic regimes. However, imprudent introductions of fish into wetlands can disrupt aquatic invertebrate communities and the link between primary consumers and consumers (Duffy 1998). Other values that wetland aquatic invertebrates provide to the GYE should be documented.

As one of the last relatively intact ecosystems in the continental United States, the GYE may be a reservoir for biological diversity (Pace 1997). Conserving biological diversity is one of the missions of the National Park System (Clark and Minta 1994). However, research in Yellowstone and Grand Teton National Parks has primarily addressed a few charismatic, economically important, or endangered species and their habitats (Yellowstone National Park 1997). The astonishing proportion (~70 percent) of taxa identified in this study that were new records for the parks supports the contention by Clark and Minta (1994) that species representing most of the biological diversity in the parks are either assumed to be doing well or ignored. Biologically diverse wetland aquatic invertebrate communities may contribute substantially to ecosystem functions other than foodweb support. The role of water fleas (Cladocera) and other filter-feeding aquatic invertebrates in maintaining water quality of lakes by removing algae is well documented (Sommer et al. 1986). These functional groups should function similarly in wetlands. Aquatic invertebrates also may play a more important role in wetland nutrient cycling than has been recognized. Aquatic invertebrates can regenerate as much as 35–60 percent of their own nutrient content each day (Lehman 1980), helping fuel algal growth and influencing algal competition by altering nutrient ratios (Sterner 1990).

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