Environmental Profile of *Tricorythodes minutus* Traver (Ephemeroptera: Tricorythidae) in the Western United States

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ABSTRACT

Based on data from 892 stations in 11 western states two geographic populations of *Tricorythodes minutus* Traver are described. The Great Basin population was found in streams that had sedimented substrate, sparse riparian vegetation, low channel gradients, and moderate to high concentrations of alkalinity and sulfates. The other population, found in California and Oregon, commonly occupied streams with moderate siltation, dense riparian vegetation, and low alkalinity and sulfate concentrations. The differences between the two populations could be the result of competitor or predator avoidance by one or both populations, or different limiting seasonal or irregular events may cause the separation. It is possible that the two populations represent subspecies or even two distinct species.

INTRODUCTION

The terms "niche breadth" (Colwell and Futuyma 1971, Pielou 1972) and "environmental tolerance" have been used almost synonymously in describing the occurrence of aquatic macroinvertebrates (Winget and Mangum 1979, Winget 1985). Prior to 1980 we considered *Tricorythodes minutus* as a tolerant mayfly species commonly found in streams subject to heavy sedimentation and severe water quality deterioration. The U. S. Environmental Protection Agency published a summary of "Environmental Requirements and Pollution Tolerance of Ephemeroptera" (Hubbard and Peters 1978) in which it was reported that *T. minutus* is found in streams throughout the western United States and Canada with pH values of seven or higher, medium to high nutrient and organic material concentrations, low to high dissolved oxygen concentrations, 15 to 30°C water temperatures, moderate to high turbidities, and slight to moderate water currents. This species is a predator, herbivore and scavenger occupying habitats ranging from mud, silt, rocks, gravel and plant substrates. It is hard to imagine a broader niche breadth than that described.

There are numerous streams in the western U. S. that naturally exhibit high pH, heavy turbidities, high temperatures and significant nutrient and

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organic loadings -- Virgin, Escalante, Pecos, Santaquin, Dirty Devil, and Muddy Rivers are a few examples. Many streams exhibit these conditions because of human perturbations, but not all. It is important to assign environmental tolerances to aquatic invertebrates based upon natural conditions as well as perturbations.

In the early 1980's we analyzed sample data from Oregon and California that indicated *T. minutus* also occurs in streams with high quality water, coarse rocky substrates and dense riparian vegetation. It was obvious that a closer look at this species was needed. Could *T. minutus* include more than one species? As reported by Edmunds, Jensen and Berner (1976) ". . . *T. fallax* and *T. minutus* intergrade completely along the eastern borders of California, Oregon and Washington . . . At most *T. fallax* and *T. minutus* seem worthy of subspecific rank, but we believe that these will best be regarded as mere clinal variants and hereby designate *fallax* as a synonym of *minutus*." Edmunds and Allen (1957) had already synonymized *T. fallacina* McDunnough with *T. minutus* Traver.

The purpose of this paper is to present a new look at the environmental profile of *T. minutus*.

METHODS

The same methods and data base used to described the environmental profile of a related mayfly, *Drunella doddsi* (Mangum and Winget 1991), were used in this paper.

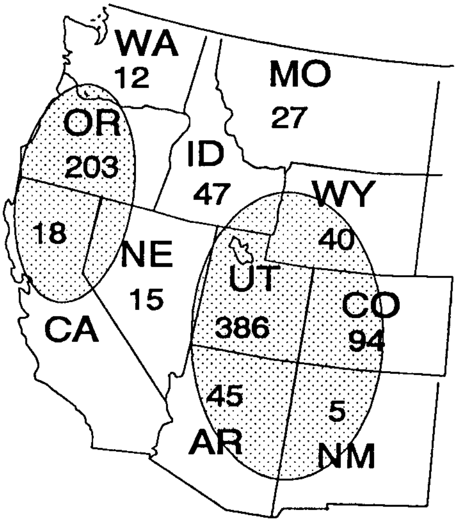

Figure 1. Number of sampling stations per state. Shading shows distribution of *T. minutus*.

Data from stream surveys collected during 1972 through 1989 by the Aquatic Ecosystem Analysis Laboratory (U. S. D. A., Forest Service, Intermountain Region, Ogden, Utah) and the Aquatic Ecology Laboratory (Brigham Young University, Provo, Utah) were used for these analyses. In eleven western states, 892 stream stations were surveyed (Fig. 1) as to habitat, water quality and composition of macroinvertebrate communities.

During early stages of this study (1972-79)statistical analyses of correlations between species richness and various environmental conditions at 164 stations were made. Several water quality parameters were eliminated because of extreme temporal fluctuations or repetitive or insignificant correlations. Total dissolved solids, nitrogen and phosphorous species, pH, turbidity and dissolved oxygen were among those eliminated. Based upon these preliminary results, five variables were selected for the final analysis (Winget and Mangum 1979).

1). Percent stream gradient was selected because of its positive correlation with macroinvertebrate community diversity (r=+0.520, P<0.001). Gradient is related to water velocity, and as Wesche (1985) reported, referring to works of Scott (1958) and Allen (1959), ". . . velocity is the most important parameter in determining distributional patterns of aquatic invertebrates." Hynes (1970) reported that velocity is directly effected by gradient of the channel and fluctuates rapidly and frequently in most streams. Gradients were measured 100 meters upstream and down from sampling site.

2). Stream substrate composition was selected because of significant correlations with community diversity. Boulder and rubble each showed positive correlation with number of taxa (r=+0.402, P<0.001, and r=+0.414, P<0.001, respectively). Correlation between gravel and species richness was not significant (r=-0.165, P>0.05), but sand/silt showed a negative correlation of r=-0.590, P<0.001. Each of four categories of substrates - boulder, rubble, gravel, fines - were recorded as to their dominance, first through fourth, at each station.

3). Alkalinity was selected because of a significant negative correlation with species richness (r=-0.668, P<0.001. Measurements used are averages of early summer (July-August) total alkalinity. Flows in July-August are generally more stable and do not include annual maximum (spring runoff) or minimum (late winter) flows. Alkalinity values vary indirectly to stream discharge.

4). Sulfate concentrations exhibited a negative correlation with species richness of r=-0.420, P<0.001. Sulfate measurements are average summer (July-August) values, as described for alkalinity.

5). Riparian vegetation was selected because of correlations with species richness at study stations -- evergreen trees, r=+0.535, P<0.001); deciduous trees, r=+0.017, P>0.05; brush, r=-0.032, P>0.05; grasses, r=-0.114, P>0.05; and bare soil, r=-0.439, P<0.001. Each riparian vegetation class was recorded as to dominance of bank cover at each station.

Stream station elevations and average minimum flows were selected because of their importance in describing station location and general characteristics. Minimum flows were averaged over the years of record to avoid impacts of infrequent hydrological events. Because of similar correlations of sulfates, total dissolved solids and specific conductance with species richness, specific conductance was included as a backup for stations for which sulfate data were not available and total dissolved solids data were not used.

Environmental variables were ranked into classes. The number of stations per variable may be less than total stations sampled because of incomplete data for that variable. Relative frequency is the number within a class divided by the total number of stations for that variable -- e.g. the relative frequency of stations that have elevations between 2000 and 4000 feet is the number of such stations divided by the total number of stations with elevation data.

Differences between relative frequencies of stations where *T. minutus* was collected and the total environmental array open to colonization were analyzed. Significance of differences, or "goodness-of-fit" was determined using the chi-square analysis (Elliott 1977, Ludwig and Reynolds 1988). Significance indicate a distribution other than random of *T. minutus* in relation to the independent variable being analyzed. Distribution of *T. minutus* may be in response to variables tested or reflect action/s of other related variables.

RESULTS AND DISCUSSION

Tricorythodes minutus was collected from near sea level to over 9,000 feet elevation. Between 2,000 and 6,000 feet, frequencies of occurrence were significantly higher than expected and less than expected at elevations over 6,000 feet (Table 1). There appears to be two populations of *T. minutus* in the study area (Figure 1). The population in Oregon and California is called the western and the other, the Great Basin population.

Size of average minimum stream flow did not seem to affect distribution of *T. minutus*. Nymphs of *T. minutus*, although collected from all gradient classes, were collected more frequently than was expected from streams with channel gradients less than two percent (Table 1). *Tricorythodes minutus* was collected from only four of 80 stations with gradients over four percent, significantly less than expected. Distributions according to gradient were not significantly different between the western and Great Basin populations.

Stations with 50 mg/l or less alkalinity accounted for 27.6 percent of all stations sampled while only 9.7 percent of the stations *T. minutus* was collected from had alkalinities that low (Table 2). Occurrence of *T. minutus* nymphs in both the western and Great Basin populations were higher than expected at alkalinities from 150-350 mg/l, but the relationship was stronger in the Great Basin than the western population. The average alkalinity for Great Basin stations was 206 mg/l and 149 mg/l for western stations.

Only 26.2 percent of all stations sampled had sulfate concentrations over 50 mg/l, but 56.9 percent of stations with *T. minutus* were in this group (Table 2). Stations in the western population area averaged 9 mg/l sulfate compared to 335 mg/l in the Great Basin area. Related to sulfates, distribution of *T. minutus* was random in the western population but distribution of the Great Basin population was significantly different than random, the same as shown in Table 2. Specific conductance had similar correlations as sulfates.

Tricorythodes minutus was found at lower than expected frequencies at stations dominated by boulder, and higher than expected frequencies at stations dominated by fine-sized substrates (Table 3). The differences between occurrence of substrate categories at all stations and those *T. minutus* was collected from are significant, but not highly significant (P=0.1). When boulders were abundant, occurrence of western *T. minutus* was random, but at similar stations in the Great Basin occurrence was significantly less than expected. When fines were dominant, distribution of *T. minutus* was random in the western area, but higher than expected in the Great Basin (P=0.025).

Table 1. Distribution of stations according to elevation, minimum stream flows, percent channel gradient and occurrence of *Tricorythodes minutus*. Goodness of fit was measured with a chi-square analysis. ns = not significant; * = 0.1; ** = 0.01; *** = 0.001

Station Variable	Total Number of Stations		Stations with *T. minutus*		Chi-Square Values
	No.	Rel. Freq.	No.	Rel. Freq.	
Elevation in Feet Above Sea Level					
≤2000 ft	52	0.067	20	0.079	0.57ns
-4000 ft	131	0.169	64	0.254	10.82+**
-5000 ft	108	0.139	49	0.194	5.53+*
-6000 ft	135	0.135	57	0.226	3.95+*
-7000 ft	114	0.147	25	0.099	3.90-*
-8000 ft	107	0.138	18	0.071	8.07-**
-9000 ft	78	0.100	13	0.052	6.00-*
>9000 ft	51	0.066	6	0.024	6.74-**
Minimum Stream Flows - cfs					
≤ 0.5 cfs	49	0.113	10	0.064	3.37-*
- 1 cfs	64	0.147	28	0.178	1.02ns
- 2 cfs	49	0.113	22	0.140	1.03ns
- 5 cfs	106	0.244	39	0.248	0.01ns
- 15 cfs	79	0.182	32	0.204	0.41ns
> 15 cfs	87	0.200	26	0.166	0.93ns
Percent Stream Channel Gradient					
≤ 1%	225	0.309	93	0.425	9.39+**
- 2%	215	0.296	81	0.370	4.07+*
- 3%	135	0.186	32	0.146	1.85ns
- 4%	72	0.099	9	0.041	7.42-**
- 5%	49	0.067	2	0.009	11.03-***
> 5%	31	0.043	2	0.009	5.84-*

Distribution of *T. minutus* in relation to riparian vegetation cover was not random (Table 4). The most significant positive differences were at stations where riparian vegetation was either lacking or grass was dominant. Occurrence of *T. minutus* was less than expected at stations that had dense riparian vegetation with grass lacking and trees dominant. In the western area, occurrence of *T. minutus* in relation to riparian vegetation at stations was random except for a higher than expected occurrence (P=0.005) when deciduous trees were absent. Great Basin population showed similar distributional relationships as shown in Table 4, except for a significantly lower than expected occurrence when coniferous trees were dominant (P=0.005). In the Great Basin conifers are generally present at higher elevation streams that have rocky substrates and high channel gradients. The significant negative relationship between coniferous trees is probably a reflection of these factors rather than the trees themselves. Lack of riparian vegetation is usually indicative of desert conditions and/or overgrazing impacts which result in a sedimented channel. *Tricorythodes minutus* appears more tolerant to sedimentation than many taxa. This could explain the significant correlations between distribution and lack of riparian vegetation.

Table 2. Distribution of stations according to alkalinity, sulfate, and specific conductance levels and occurrence of *Tricorythodes minutus*. Goodness of fit was measured with a chi-square analysis: ns = not significant; * = 0.1; ** = 0.01; *** = 0.001

Station Variable	Total Number of Stations		Stations with *T. minutus*		Chi-Square Values
	No.	**\ Rel. Freq.**	**No.**	**\ Rel. Freq.**	
Total Alkalinity as mg/l $CaCO_3$					
≤ 50	206	0.276	23	0.097	27.53-***
- 100	145	0.194	35	0.148	2.66ns
- 150	111	0.149	29	0.122	1.11ns
- 200	94	0.126	49	0.207	12.26+***
- 250	67	0.090	38	0.160	13.13+***
- 300	48	0.064	25	0.105	6.23+*
- 350	47	0.063	24	0.101	5.51+*
> 350	28	0.038	14	0..059	2.93ns
Sulfate as mg/l					
≤ 10	315	0.467	52	0.255	19.60-***
- 25	126	0.187	38	0.186	0.00ns
- 50	57	0.084	25	0.122	3.51+*
- 75	40	0.059	13	0.196	0.07ns
> 75	137	0.203	76	0.373	28.90+***
Specific Conductance as mhos/cm					
≤ 100	150	0.238	16	0.076	23.19-***
- 200	124	0.197	33	0.157	1.70ns
- 300	64	0.102	21	0.100	0.01ns
- 400	60	0.095	20	0.095	0.00ns
- 600	86	0.137	44	0.210	8.14+**
- 800	47	0.075	23	0.110	3.40+*
> 800	98	0.156	53	0.252	12.58+***

Table 3. Distribution of stations according to dominance of substrate classes and occurrence of *Tricorythodes minutus*. Goodness of fit measured with a chi-square anlaysis: ns = not significant; * = 0.1; * = 0.01; *** = 0.001

Station Variable	Total Number of Stations		Stations with *T. minutus*		Chi-Square Values
	No.	**Rel. Freq.**	**No.**	**Rel. Freq.**	
Boulder Substrate					
1	62	0.076	10	0.040	4.26-*
2	142	0.175	33	0.133	2.53ns
3	130	0.160	40	0.161	0.01ns
4	479	0.589	166	0.667	2.54ns
Rubble Substrate					
1	372	0.458	98	0.394	2.23ns
2	213	0.262	59	0.237	0.60ns
3	154	0.189	59	0.237	2.97+*
4	74	0.091	33	0.133	4.71+*
Gravel Substrate					
1	218	0.268	69	0.277	0.08ns
2	298	0.367	98	0.394	0.50ns
3	224	0.276	54	0.217	3.11-*
4	73	0.090	28	0.112	1.42ns
Fine-Sized (Sand, Silt & Clay) Substrates					
1	154	0.189	70	0.281	11.20+***
2	165	0.203	56	0.225	0.00ns
3	235	0.289	73	0.293	0.57ns
4	259	0.319	50	0.201	10.91***

Distribution of a species based upon selected variables illustrates trends, but there are frequently confounding effects with one variable modifying the response of a species to another variable. An example of this is illustrated in Figure 2. We selected eleven stream stations in California and Oregon from which *T. minutus* had been collected. These stations were selected because they had approximately the same water quality -- streams in these states reflect less water quality variation than streams in the Great Basin. We divided these streams according to condition of substrates and riparian vegetation. According to data presented above, *T. minutus* would most likely be collected from stations with sparse riparian vegetation and fine substrates and least likely be collected where vegetation is dense brush and trees and substrates mostly coarse rocks. *Tricorythodes minutus* occurred in only six of 14 collections and in low densities from the three streams where substrates were coarse and vegetation dense. At the three stream stations where vegetation was still dense but substrates were mostly sand and silt, *T. minutus* was present in 11 of 12 collections and densities ranged from low to high. At the five stream stations that had sparse vegetation and primarily fine substrates, *T. minutus* was present in all 11 collections and in high densities. Frequency and densities increased as the variables approached those most often associated with *T. minutus* occurrence.

Table 4. Distribution of stations according to dominance of riparian vegetation classes and occurrence of *Tricorythodes minutus*. Goodness of fit measured with a chi-square anlaysis: ns = not significant; * = 0.1; * = 0.01; *** = 0.001

Station Variable	Total Number of Stations **No. **	**Rel. Freq.**	Stations with *T.minutus* **No. **	**Rel. Freq.**	Chi-Square Values
Riparian Vegetation Lacking					
1	106	0.137	33	0.135	0.01ns
2	106	0.137	44	0.180	3.22+*
3	109	0.141	53	0.216	9.86+**
4	102	0.132	34	0.139	0.09ns
5	350	0.453	81	0.331	8.08-**
Grass Vegetation					
1	277	0.358	117	0.478	9.72+**
2	151	0.195	48	0.196	0.00ns
3	153	0.198	46	0.188	0.13ns
4	133	0.172	23	0.094	8.70-**
5	59	0.076	11	0.045	3.17-*
Brush Vegetation					
1	209	0.270	65	0.265	0.02ns
2	300	0.388	102	0.416	0.50ns
3	166	0.215	45	0.184	1.10ns
4	31	0.040	10	0.041	0.01ns
5	67	0.087	23	0.094	0.15ns
Deciduous Tree Vegetation					
1	111	0.144	22	0.090	4.94-*
2	124	0.160	31	0.127	1.75ns
3	145	0.188	43	0.176	0.19ns
4	143	0.185	57	0.233	3.01+*
5	250	0.323	92	0.376	2.06ns
Coniferous Tree Vegetation					
1	63	0.082	7	0.029	8.42-**
2	82	0.106	20	0.082	1.38ns
3	119	0.154	30	0.122	1.58ns
4	102	0.132	28	0.114	0.58ns
5	407	0.527	160	0.653	7.45+**

Tricorythodes minutus occurs in a wide range of conditions, but frequency of occurrence and density of nymphs are highest when riparian vegetation is sparse and substrates are sedimented; when alkalinities, specific conductance and sulfates are high; and when channel gradients are low. These conditions are often indicative of stressed stream systems, at least in the mountainous western United States. Whether *T. minutus* selects for these conditions directly or because they are related to other factors not measured, such as fewer competitors present, is not known.

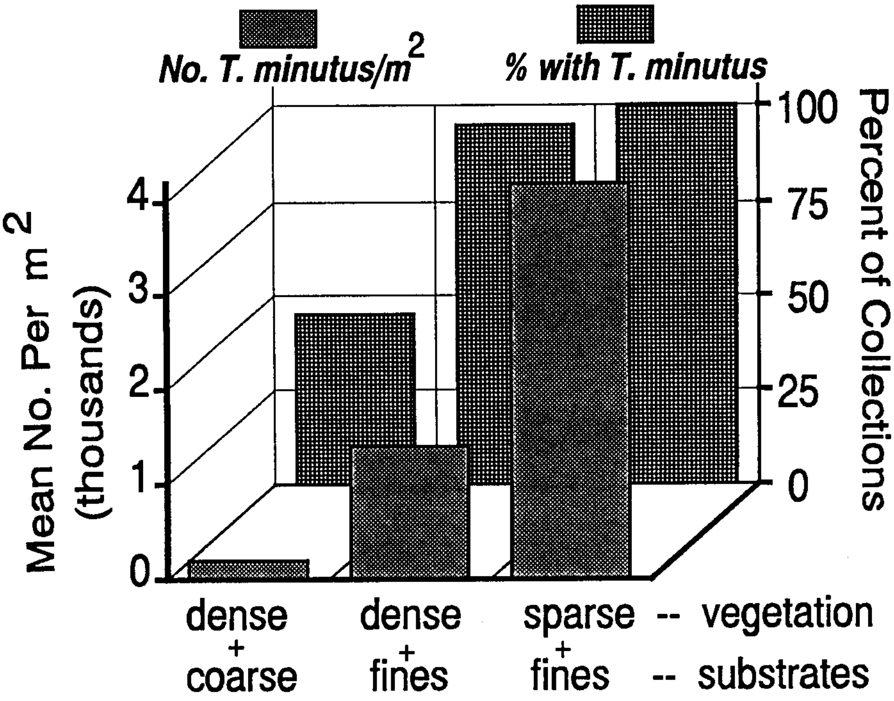

Figure 2. Frequency of occurrence and mean density of *T. minutus* at eleven stream stations with similar water quality.

It is interesting that the western population *T. minutus* frequently occurs in streams with low alkalinity (10-25 mg/l) and sulfate (2-10 mg/l) concentrations, but in the Great Basin, streams with similar water quality rarely have *T. minutus* in them. A related species of mayfly, *Drunella doddsi*, is found throughout both population areas, but it exhibits a similar niche width in both (Mangum and Winget 1991). *Drunella doddsi* has a significantly negative (P<0.001) co-occurrence with *T. minutus*, especially in the Great Basin. For example, in Utah streams with sulfates less than 25 and alkalinities less than 100, *T. minutus* occurs infrequently, but *Drunella doddsi* is very common. On the other hand, *T. minutus* is common in streams with alkalinities over 350 mg/l and sulfates over 2,000 mg/l, but *D. doddsi* is never found in these streams. Most of the streams these two species share are in the western population area.

Why is *T. minutus* not more widespread, considering its broad niche width? Why is *T. minutus* absent from streams in the Great Basin similar to those it inhabits in the western area? Could it be the result of competitor or predator avoidance by one or both populations? Could absence from some streams be the result of different seasonal or irregular disturbances in each area (Resh et. al 1988) such as thunderstorm floods, scour ice, or near dewatering of streams during droughts. Could the two populations be separate species or subspecies with differing adaptations. It is obvious that *T. minutus* is a plastic species, physiologically and morphologically capable of occupying a wide variety of environments. *Tricorythodes minutus* is a tolerant species.

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