Habitat Partitioning among Three Species of Ephemerelloidea

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ABSTRACT

Niche volumes according to several physical and water quality parameters are shown for *Drunella grandis, Drunella doddsi* and *Tricorythodes minutus.* Generalist strategies have been adopted by *D. grandis* for physical habitat characteristics and by *T. minutus* for water quality characteristics. *Drunella doddsi,* a specialist, has the smallest physical habitat and water quality niche dimensions of the three mayfly species. Even though each has its own unique niche, there is some overlap between them for most niche dimensions studied. These overlaps are probably present because density independent seasonal limiting factors in western United States streams are as strong or stronger selectors than many density dependent factors. Also, each species has its own unique niche "hypervolume" that changes from station to station and from time to time.

INTRODUCTION

Organisms have numerous choices as to how they are going to allocate their time and energy to meet environmental demands. Species will establish unique niches by partitioning resources in many ways. Pianka (1988), quoting Hutchinson (1957) refers to a niche as an n-dimensional hypervolume because of the many variables or dimensions involved. He points out that niches may be overlapping along one axis and yet be completely separated along another. He further explains that because of the multidimensional nature of niches, a species can be under considerable competitive pressure from the summed small niche overlaps of many neighboring species. This "diffuse" competition could exert as much or more pressure for habitat or resource partitioning than larger niche overlaps by a few competing species in the community. This results in realized multidimensional niches impossible to completely describe without knowing everything about the species involved.

Food and substrate are the most common dimensions used to describe niche width in aquatic ecology. The use of food to describe niche overlap has some serious drawbacks. Partitioning of food resources among species probably results from long-term competition among these species for limited food resources. Short (1983) reported no significant partitioning of food resources in a Colorado trout stream among six species of mayflies, including *D. grandis.* Rader and Ward (1987) reported that in a Colorado mountain stream six mayfly species did not partition food resources by varied temporal sequencing of peak food resource utilization.

Competition for food is a density dependent relationship, increasing as density of competing populations increase. Lack of food resource partitioning in a stream

system is evidence that population density does not generally reach a point where food is a primary limiting factor. Also, as reported by Hawkins (1985) diets differ among individuals of a single species, especially among individuals of different sizes and/or occupying different habitats. Rader and Ward (1989) reported that *Drunella grandis* nymphs were detritus eaters above an impoundment on the Little Colorado River but switched to a mainly diatom diet below the impoundment where detritus was limited.

Aquatic invertebrate populations in mountain streams are more frequently limited by physical/chemical factors than by either food or space. In intermountain streams, low water flows, either summer or winter, commonly limit macroinvertebrate density and distribution. Scouring flows following spring snow melt or heavy summer thunder storms, scour ice, irrigation diversions, high summer water temperatures, and heavy algal growths are other common limiting factors. Schoener (1974), after studying over 80 natural communities, came to the conclusion that macrohabitat dimensions are generally more important in separating niches than microhabitat, food types or temporal activities. Hawkins (1984) reported that habitat specialization appeared to be a major force behind adaptive radiation within species of Ephemerellidae.

Pianka (1988) stated: "Organisms stressed along any one environmental variable are thus able to tolerate a lesser range of conditions along other environmental variables." For example, an organism stressed by increasing sedimentation will not be able to tolerate as much dissolved solids or increased water temperatures as it would if substrates were free from sand and silt. Of course the opposite is also true -- lack of stress in several variables will increase an organism's tolerance to greater ranges of conditions in another variable. A single species will actually have numerous realized niches. Its niche will change both in time at any given place and also from place to place. This helps explain why species occasionally utilize resources not usually used or why they occur at stations with one or two environmental conditions considered beyond their tolerance ranges. It also explains why it is so difficult to describe a tight environmental profile for most species.

Realizing that niches have many dimensions, not only habitat related but also behavioral and temporal related partitioning, it seems obvious that the hypervolume of a niche for any given species is not a static thing but rather takes on different characteristics as it moves through time and space. In this paper I attempt to show niche separation of three species of mayflies based upon selected horizontal or macrohabitat niche dimensions. The three species compared in this paper, *Drunella doddsi* Needham, *Drunella grandis* Eaton and *Tricorythodes minutus* Traver, all belong to the Superfamily Ephemerelloidea (Edmunds, Jensen and Berner 1976). All three species are clingers/sprawlers, collectors/gatherers, and feed on detritus. Mangum and Winget (1991), Winget and Mangum (1991) and Mangum and Winget (1993) have published environmental profiles of *D. doddsi*, *T. minutus*, and *D. grandis*, respectively. While this paper is largely a synthesis of those three reports, it presents a valuable synthesis of the functional descriptor -- the niche hypervolume.

RESULTS AND DISCUSSION

Of the 898 stream stations surveyed in this study, 641 (71.4%) had one or more of these mayflies present. Each species was widely distributed (Table 1). *Drunella doddsi* was found at 309 stations, *D. grandis* at 246 stations and *T. minutus* at 264 stations. All three species were found at only 17 stations. Results of a Jaccard Similarity Coefficient analysis in 1991 (898 stations in 11 western states) illustrates low co-occurrences among these species: 0.053 for *D. doddsi:T. minutus*, 0.128 for *D. grandis:T. minutus*, and 0.233 for *D. doddsi:D. grandis* (Fig. 1). A similar analysis in 1979 (100 stations mostly in Utah) showed different results illustrating the importance of a broad geographical data base for analyses of this type. Interspecific Association Coefficient analysis (Ratliff 1982) show a strong divergence of habitat selection among *T. minutus* and both *D. doddsi* and *D. grandis* (IAC = -0.6721 and IAC = -0.201, respectively). Co-occurrence between *D. doddsi* and *D. grandis* was weakly positive (IAC = +0.090)

Table 1. Occurrence of three species of mayflies at stream stations in 11 western states, 1972 through 1991.

State (# stns)	D. grandis	D. doddsi	T. minutus
Arizona (45)	15	1	25
California (18)	6	12	7
Colorado (94)	39	43	38
Idaho (47)	22	29	3
Montana (27)	18	12	0
Nevada (15)	7	6	0
New Mexico (5)	0	2	1
Oregon (203)	44	74	67
Utah (386)	95	98	119
Washington (12)	1	2	0
TOTAL	246	309	264
Co-occurrence			
grandis + doddsi	105		
grandis + minutus	58		
doddsi + minutus	30		
grandis + doddsi + minutus	17		

indicating less divergence between these two species. These results support the 1991 Jaccard Similarity Coefficient analysis.
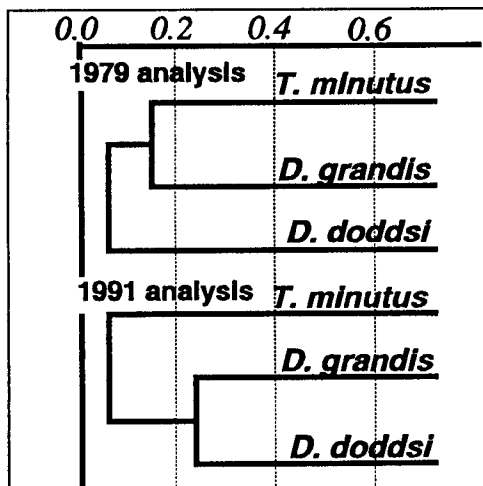

Figure 1. Co-occurrence of three species of mayflies from two sets of data.

It is obvious that *T. minutus* has diverged more in physical/chemical requirements from the other two species than *D. grandis* and *D. doddsi* have diverged from each other. This is expected since, based upon taxonomic evaluations (morphological and evolutionary) they are placed in two separate families (*T. minutus* in Tricorythidae and *D. grandis* and *D. doddsi* in Ephemerellidae).

Figures two, three and four illustrate six niche dimensions for these three species of mayflies. Shown are total ranges including: portions where each species is found less than would be expected under random

distributions (able to tolerate under certain conditions, but an avoidance is obvious); portions where each species is found at frequencies if distributions were random (environmental variable probably not very important in deciding distributions); and portions where occurrences are in frequencies higher than expected under random distribution (species actively selecting for those conditions).

Figure 2. Occurrence of three species of mayflies according to elevation (a) and percent channel gradient (b).

All three species were found throughout the elevational range of the study, but *D. doddsi* and *D. grandis* were found more than expected at higher elevations. *Drunella doddsi* had the narrowest range (Fig 2). *Tricorythodes minutus* was found most often at elevations below 6,000 ft. Ward and Berner (1980) found similar elevational partitioning of Vrain Creek, Colorado by these three species.

Each species was found commonly over a broad range of stream channel gradients (Fig. 2). *Drunella grandis* was more of a generalist in overall stream gradients inhabited, while *D. doddsi* specialized for steeper gradients, and *T. minutus* preferred flatter stream channels. The greatest specialization was by *T. minutus*, which was only rarely found in streams with three percent or greater gradients.

Drunella grandis was a generalist for substrate utilization with its frequency of occurrence being random for almost all substrate types. *Drunella doddsi* was specialized for life on coarse substrates, and *T. minutus* opted for sand/silt substrates (Fig. 3).

Streamside vegetation appeared to have little effect on distribution of *D. grandis*, while *D. doddsi* was more frequently found at stations with dense tree and shrub riparian cover. *Tricorythodes*
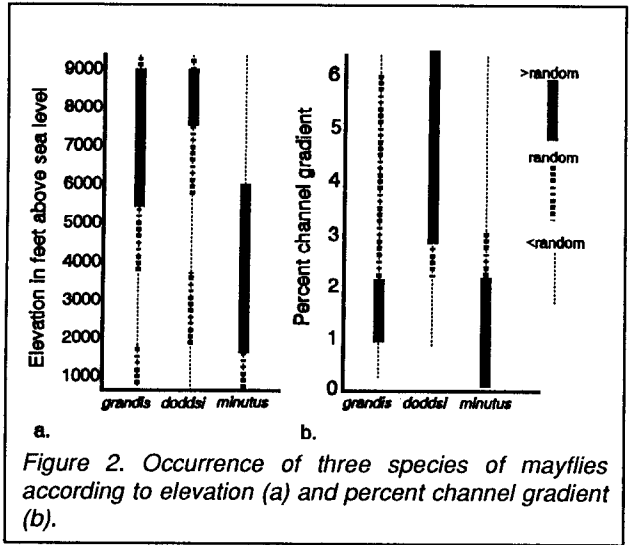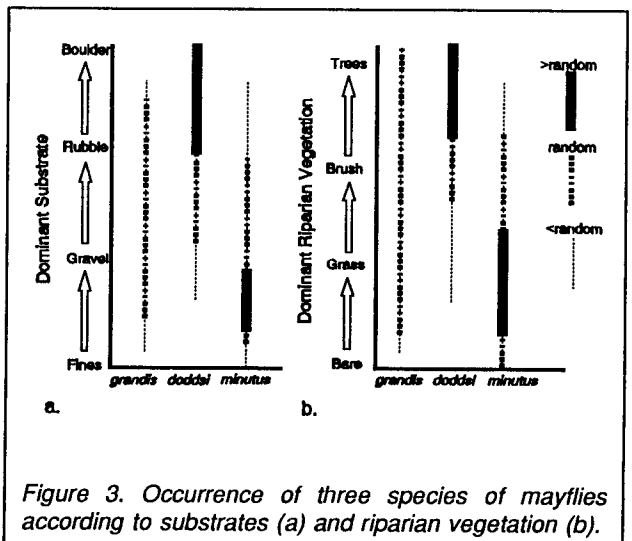

Figure 3. Occurrence of three species of mayflies according to substrates (a) and riparian vegetation (b).

minutus most commonly occupied stations with sparse stream bank cover (Fig. 3).

Frequency of occurrence of these three mayflies at various concentrations of alkalinity and sulfate show *D. grandis* and *D. doddsi* have selected for narrow ranges for both water chemical parameters (Fig. 4). *Tricorythodes minutus* shows not only a tolerance for almost all alkalinity and sulfate levels but a selection for high concentrations of these chemicals in stream waters.
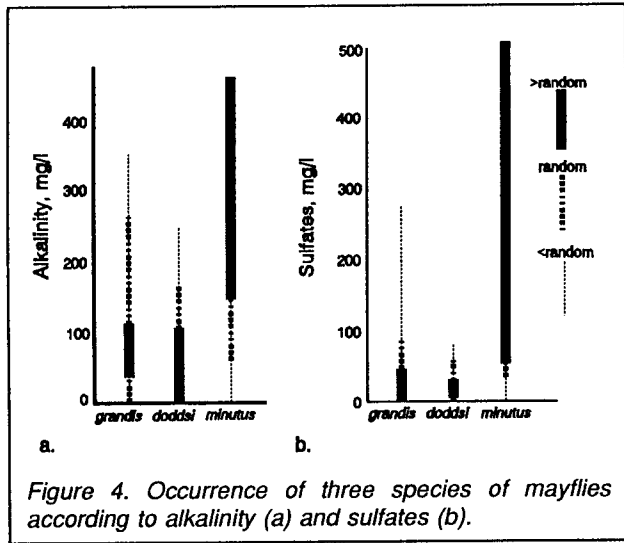

Figure 4. Occurrence of three species of mayflies according to alkalinity (a) and sulfates (b).

Pianka (1988) referred to a niche as a hypervolume because of the many dimensions involved resulting in complex relationships among community members. He pointed out that niches of several species may be overlapping along one axis and yet be completely separated along another. He further contended
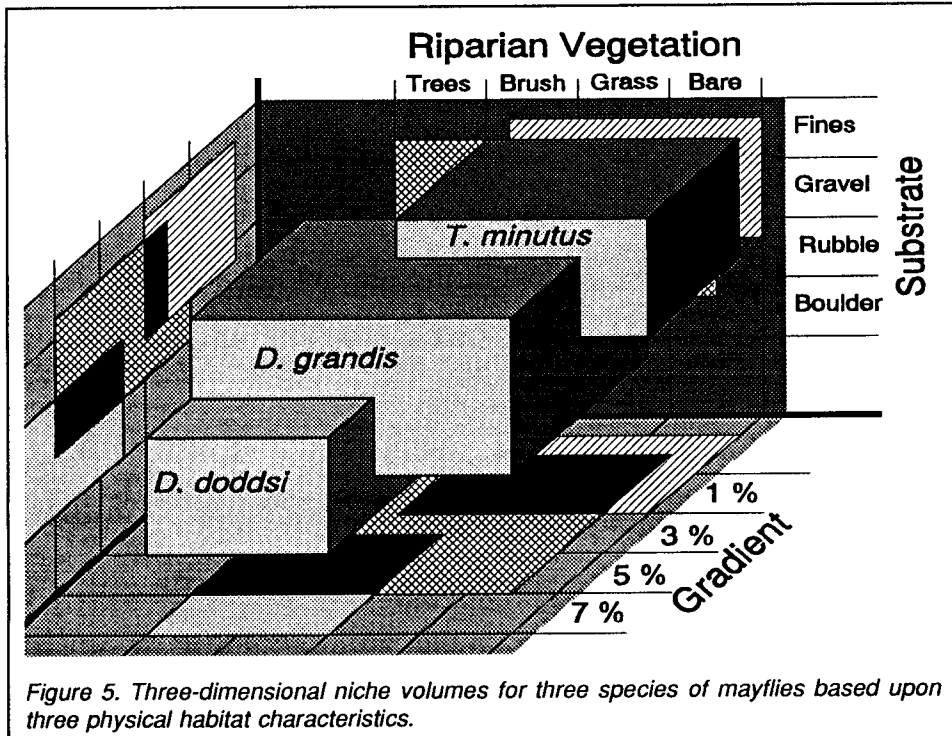

Figure 5. Three-dimensional niche volumes for three species of mayflies based upon three physical habitat characteristics.
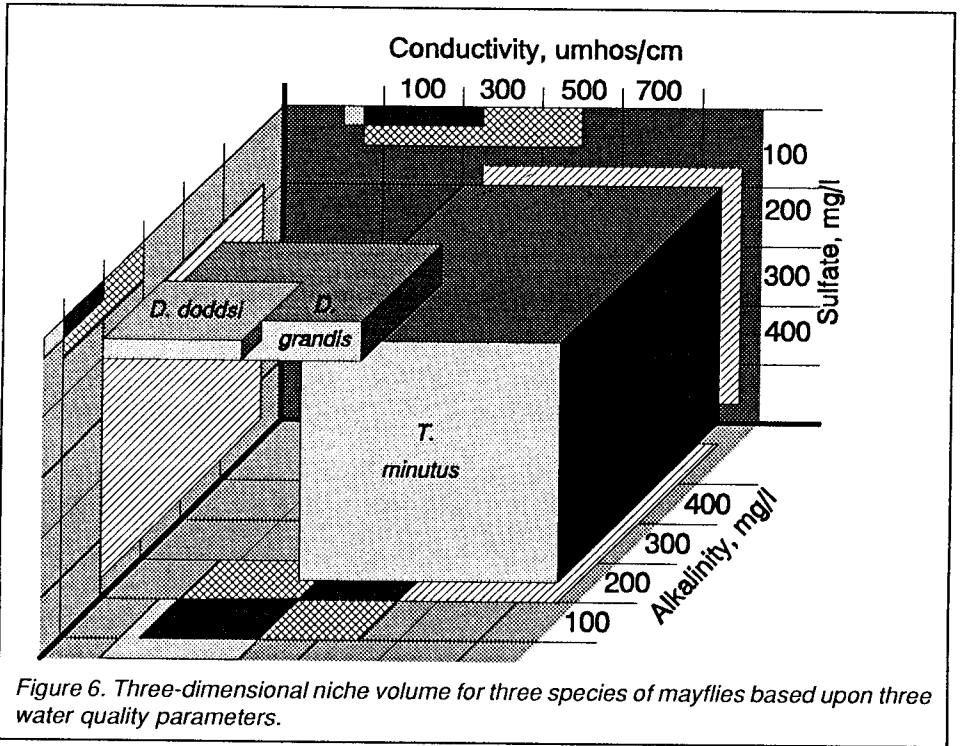
Figure 6. Three-dimensional niche volume for three species of mayflies based upon three water quality parameters.

that highly specialized organisms usually have narrow tolerance limits along one or more niche dimensions. Three-dimensional representations of niche volumes help illustrate this dynamic concept. The shape and overlap of niche volumes depends upon the niche dimensions selected for each analysis.

When comparing riparian vegetation, substrate and stream channel gradient dimensions, *D. grandis*, obviously a generalist in selecting for physical habitat characteristics, shows the largest niche volume with moderate overlap with both *D. doddsi* and *T. minutus* (Fig. 5). The two latter species, each moderate specialists in physical habitat selection, show no niche overlap with each other. But when three water quality parameters are selected as niche widths (alkalinity, sulfate and conductivity) *T. minutus* is apparently a generalist according to water quality with the largest niche volume. There is no overlap among *T. minutus* and either of the two other species (Fig. 6). *Drunella doddsi* with the smallest volume and *D. grandis* with a moderately small volume both show specialist strategies with considerable overlap among the two species.

SUMMARY

There is considerable divergence among *D. grandis*, *D. doddsi* and *T. minutus*. *Drunella grandis* is randomly distributed over almost all physical habitat characteristics, a generalist strategy, but is a specialist in selecting for high quality waters. *Drunella doddsi* is a specialist in selecting both physical and chemical habitat characteristics. *Tricorythodes minutus* shows a weak specialist strategy in

selecting low gradient, sedimented streams but is a generalist in relation to water quality conditions. These three species of mayflies have noticeably diverged in several niche dimensions, but some overlap is present in most dimensions studied. These overlaps will probably always be present because density **independent** seasonal limiting factors in western United States streams are as strong or stronger selectors than many density **dependent** factors. Also, each species has its own unique niche **"hypervolume"** at each stream station because of the unique combination of environmental conditions and community structure at each station. This means that a species' niche "hypervolume" changes from station to station and also from time to time. Therefore niche dimensions should be described as frequencies or probabilities rather than absolutes.

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