Use of detrended correspondence analysis to evaluate factors controlling spatial distribution of benthic insects

Harry V. Leland, James L. Carter & Steven V. Fend
U.S. Geological Survey, 345 Middlefield Road, Menlo Park, CA 94025, U.S.A.

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Abstract

Detrended correspondence analysis (DCA) was evaluated for its effectiveness in displaying factors controlling the spatial distribution of benthic insects in an oligotrophic stream where an experimental gradient (copper) that selectively affects population abundances was imposed. DCA proved to be highly sensitive to differences among samples and consistently provided ecologically meaningful species ordinations.

Seasonality of taxa was the major gradient displayed by DCA prior to copper exposure when data for all sampling dates were included. Sensitivity of taxa to copper was a more important factor affecting community structure than was seasonality during periods of continuous exposure to copper (2.5 to 15 $\mu g\ l^{-1}\ Cu_T$; approximately 12 to 75 $ng\ l^{-1}\ Cu^{2+}$. When pre-dose data for each sampling date were ordinated independently, substratum composition and biological interactions were the major gradients displayed in species ordinations. During periods of exposure, sensitivity of taxa to copper was the primary gradient. This gradient also reflected a generally greater sensitivity to copper of herbivorous than of detritivorous or predatory benthic insects. DCA revealed the persistence, eleven months after dosing ceased, of differences in community structure between the control and high treatment (5 and 10 $\mu g\ l^{-1}\ Cu_T$) sections. Differences between sections were not evident on this sampling date from total biomass or total density (numerical) estimates.

Introduction

A common objective in water pollution investigations is to identify major factors influencing the spatial distribution of species. Where pollution effects on aquatic communities are pronounced, the controlling factor(s) may be evident from plots of spatial distributions of species and abiotic variables. However, such methods can be inefficient with large data sets and may be more subjective than most multivariate methods for evaluating community gradients. Multivariate methods commonly used to summarize spatial distributions of species are species diversity, direct gradient analysis, cluster analysis and ordination. An implied objective of each method is to achieve a reduction in dimensionality with minimum loss of information.

Species diversity, the most popular community statistic in water pollution investigations, is a function of the number of species present (species richness) and the evenness with which individuals are distributed among the species. The statistic contains both conceptual and practical limitations (Hurlbert, 1971). An important practical problem is that species richness and species diversity are frequently not positively correlated. Species richness may be a better measure of changes in community structure along a pollution gradient than is species diversity (Leland & Carter, 1984; Sheehan & Winner, 1984).

Direct gradient analysis displays community variables along known abiotic gradients and thus has advantages of simplicity and ease of interpretation where the controlling abiotic factor is obvious and

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measured. Cluster analysis arranges samples or species into discrete groups. Reductions in dimensionality are made assuming that species abundances are distributed discontinuously. This frequently leads to forced misclassifications. Where data are continuous, the process of clustering is more subjective than is ordination (Gauch, 1982a). Ordination is the arrangement of species and samples in a low-dimensional space such that similar entities are close by and dissimilar entities are far apart.

Ordination has proved effective in elucidating patterns in terrestrial vegetation and in displaying species distributions along complex abiotic gradients (Whittaker, 1954, 1973; Gauch, 1982a). However, its application to the study of aquatic plant and animal distributions is uncommon. Descy (1973, 1976) applied principal components analysis to algal abundance data (ordinal) to identify species that are sensitive to, tolerant of, or favored by organic pollution. Bruns *et al.* (1982) used polar ordination to summarize information on macroinvertebrate functional groups and on natural organic constituents, and to relate distribution of these complex variables to stream order. Several authors (Boesch, 1977; Green, 1979; Sundberg, 1983) have listed ordination methods of potential use in water pollution investigations.

In this study, detrended correspondence analysis (DCA), an ordination technique developed by Hill & Gauch (1980), was evaluated for its effectiveness in summarizing stream insect abundance data and for its usefulness in displaying abiotic and biotic gradients controlling the spatial distribution of species. An experimental gradient (copper) that selectively affected species abundances was imposed during the study. Leland & Carter (1985) considered the effectiveness of DCA in analyzing patterns in periphyton abundance data from the same study area. DCA was highly sensitive to differences among samples of the periphyton, and grouped species in an interpretable manner.

Study area and methods

Convict Creek is a perennial riffle-pool stream of the eastern Sierra Nevada mountains in California. The investigation was conducted where Convict Creek becomes part of the reserve of the Sierra Nevada Aquatic Research Laboratory (for map and description of the study area see Leland & Carter, 1984). Within the reserve, the mainstream is divided into four experimental sections. The sections range in length from 340 to 500 m and are similar in gradient, discharge and water quality.

A solution of cupric sulfate was continuously added from mid-September 1978 to mid-January 1979 to three of the sections to yield concentrations (± 25%) of 2.5, 7 and 15 $\mu g\ l^{-1}$ Cu_T (total filterable copper). The Cu^{2+} activities, as calculated by REDEQL2 (McDuff & Morel, 1973), were approximately 12, 35 and 75 ng l^{-1}, respectively. Concentrations of 2.5, 5 and 10 $\mu g\ l^{-1}$ Cu_T (± 25%) were maintained from mid-August 1979 to mid-August 1980 (Cu^{2+} activities of approximately 12, 25 and 50 ng l^{-1}, respectively). The fourth section was a control (no copper added).

Sampling of aquatic insects was conducted in spring, summer and autumn of the years 1977 through 1980, and again in July 1981. The same riffles (approximately 3 m by 50 m) were sampled each time. An invertebrate box sampler (Ellis-Rutter)[1] with a net of 0.35 mm mesh and an opening of 0.1 m^2 was used. Sampling was from the middle of the stream and included both upstream and downstream areas of the riffle. Three samples were taken from each riffle. Samples were preserved in 70% ethanol and sorted with the aid of sugar flotation (Anderson, 1959). All aquatic insects were identified to the lowest taxonomic level practical (genus or species, except for the family Chironomidae).

Detrended correspondence analysis (DCA) is an eigenanalysis procedure based on reciprocal averaging, a method shown by Hill (1973) to be algebraically similar to principal components analysis. However, DCA corrects for two common faults of reciprocal averaging which can complicate interpretation of axes. The first of these faults is an arch effect caused by the quadratic relationship of axis 2 on axis 1 (Hill & Gauch, 1980). The second is a distortion of ecological distances along the axes (Hill, 1979). All analyses were conducted using DECORANA (Hill, 1979), a program in the Cornell Ecology Program Series (Gauch, 1982b). Variables analyzed were population densities (individuals$\cdot$0.1 m^{-2}) of aquatic insects in riffles of the four experimental stream sections.

[1] Use of brand names is for identification only and does not constitute endorsement by the U.S. Geological Survey.

Results

Polar ordination (PO), principal components analysis (PCA), reciprocal averaging (RA) and detrended correspondence analysis (DCA), ordination methods commonly employed to analyze terrestrial plant distributions (Del Moral, 1980; Gauch, 1982a), were initially compared for their relative effectiveness at summarizing variation in benthic insect composition data and displaying a known gradient (copper sensitivity of taxa). Based upon this comparison, DCA was selected for subsequent analysis of the complete data set. Ordinations of samples from the four stream sections in September 1979, approximately three weeks after dosing began, are presented in Fig. 1. Beta diversity, the extent of species replacement along coenoclines, in this example is low (1.3 half changes [hc]), so each method was expected to produce a reasonably efficient sample ordination (Del Moral, 1980). PCA and RA express copper sensitivity as a curvilinear coenocline (Fig. 1b, c). An arch effect commonly observed in RA ordinations was evident at higher (hc > 1.5) beta diversities. The principal disadvantage of PO is the extreme effect of outliers on the distribution of synthetic variables (Fig. 1a). Interpretation of species ordinations was difficult with any of the methods except DCA because direction and degree of curvilinearity of gradients could not be determined with confidence. As DCA corrects for any curve in two-dimensional ordination space that results if species distributions are unimodal rather than linear, direction of the primary gradient can be ascertained and multispecies distributions assumed linear (Hill & Gauch, 1980). A further advantage of DCA is that axes are scaled in units of average standard deviation (sd) of species turnover (Gauch, 1982a).

Discontinuities in DCA ordinations of Convict Creek species composition data were always less than 0.5 sd and were therefore reliably estimated (Hill & Gauch, 1980). Eigenvalues for axis 2 in the above example (Fig. 1) are 0.08 for RA and 0.05 for

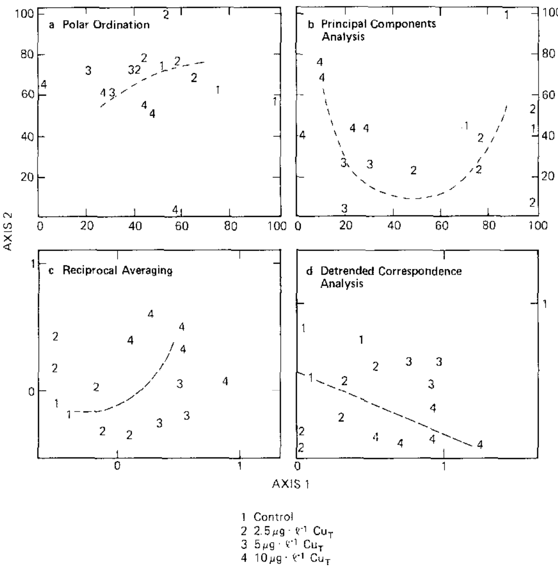

Fig. 1. Sample ordinations of population densities of benthic insects in September 1979. Dashed lines indicate direction of gradient. (a) Polar ordination using percent difference (Bray Curtis) as a distance measure (axis scale is species maximum equals 100); (b) principal components analysis with $\log_{10}$ transformed and centered data (axis scale is species maximum equals 100); (c) reciprocal averaging (axis scale is average standard deviation of species turnover); (d) detrended correspondence analysis (axis scale is average standard deviation of species turnover).

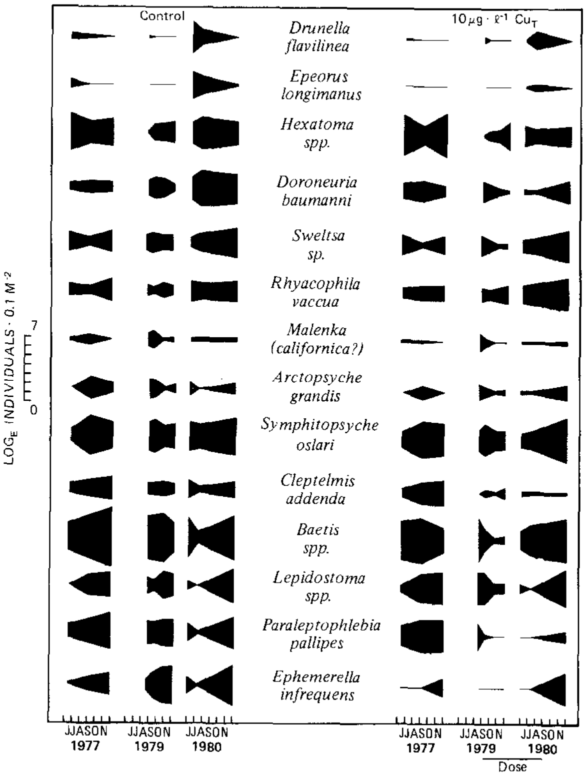

Fig. 2. Population densities of selected aquatic insects in riffle areas of the control and 10 $\mu g\ l^{-1}$ Cu_T sections of Convict Creek (dosing was from mid-August 1979 to mid-August 1980). Taxa are ordered by their location on axis 1 in DCA species ordination space (control section samples).

DCA (the eigenvalue for axis 1 is 0.31). In general, eigenvalues for axis 2 were reduced by 0.02 to 0.12 by detrending.

Mean population densities of 14 common taxa in Convict Creek are presented in Fig. 2. The taxa are ordered by their location on axis 1 of the DCA ordination of control section samples for the years 1977 through 1980. Taxa with maximum abundances in spring are represented by *Drunella flavilinea, Epeorus longimanus, Hexatoma* spp. and *Doroneuria baumanni. Malenka (californica?), Arctopsyche grandis* and *Symphitopsyche oslari* have maximum abundances in summer. Taxa with maximum abundances in autumn include *Baetis* spp., *Lepidostoma* spp., *Paraleptophlebia pallipes* and *Ephemerella infrequens.*

Ordination of the predose 1977 samples is shown in Fig. 3a. Seasonality is the major factor determing location of samples, with months grouping separately. There is no indication that the among-section variation is greater than the within-section variation. Dosing began after the August sampling

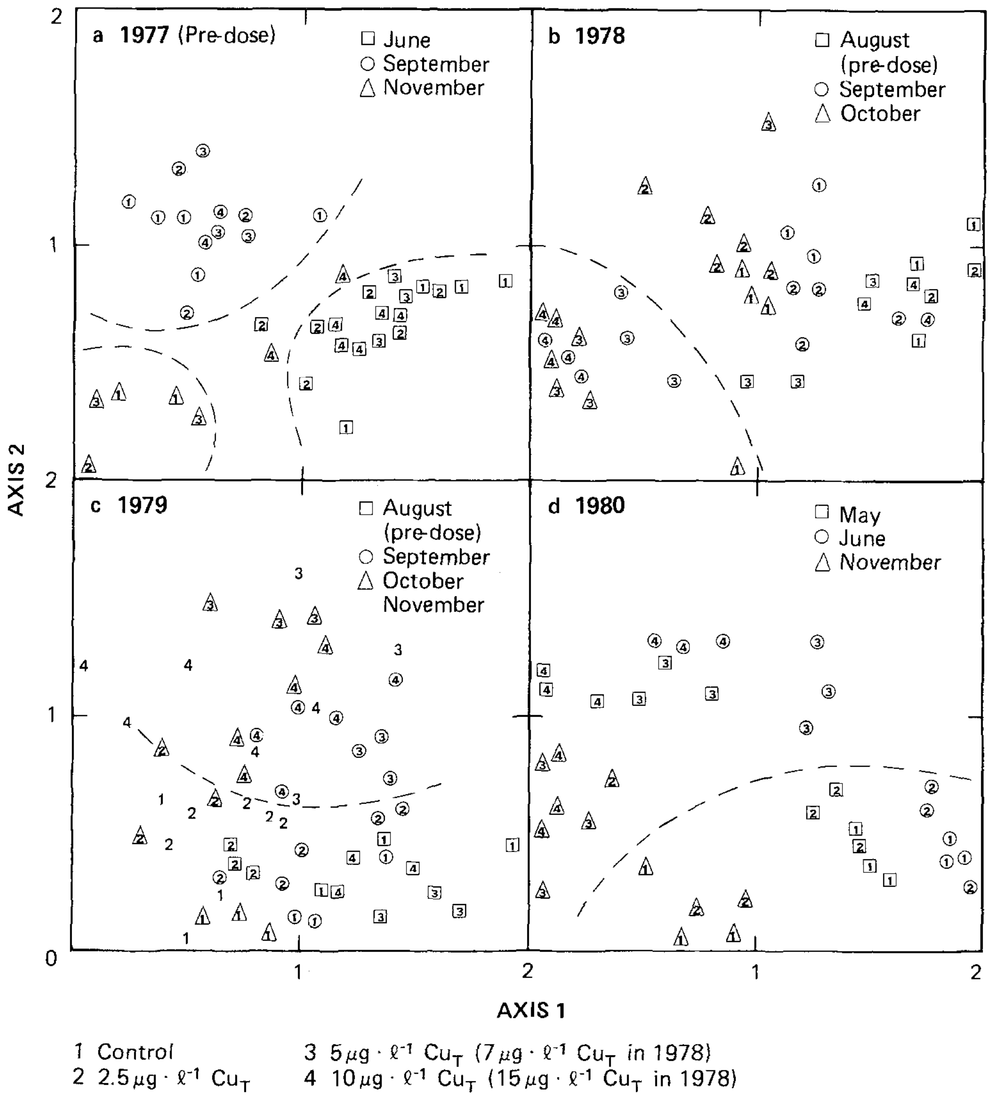

Fig. 3. Sample ordination (DCA) of population densities of aquatic insects. (a) Seasonality is expressed during the pre-dose period. (b, c, d) The axes express the seasonality and copper sensitivity of taxa (see text for details). Axis scale is average standard deviation of species turnover. November 1979 samples are plotted without an enclosing symbol. Dashed lines define groups.

in 1978. Prior to the start of dosing, there is no consistent among-section separation (squares in Fig. 3b). After dosing began, the seasonal separation apparent in 1977 disappears. The discontinuity between September and October 1978 samples is due to among-section differences in response to copper and not to seasonality. This is evidenced by the control and 2.5 μg l^{-1} Cu_T samples grouping to the upper right with the August predose samples, whereas the 7 and 15 μg l^{-1} Cu_T samples group to the lower left.

In 1979, copper dosing again began after the August sampling. A pattern develops that is similar to but less distinct than the 1978 ordination. There is a general ordering from low copper sections to high copper sections, with the August (pre-dose 1979) samples grouping with the low copper samples of later sampling dates. The ordination of 1980 samples shows a gradient from low copper (in the lower right of the figure) to high copper concentrations (in the upper left). There was no pre-dose period in 1980. Seasonality is expressed in the 1980 ordination on a diagonal gradient perpendicular to the copper gradient.

Differences among control and copper-treated sections were determined by ordinating data for each sampling date independently. Sample ordinations for representative pre-dose, dose and post-dose periods are presented in Fig. 4. There is apparently no discontinuity or ordering among samples in September 1977. A discontinuity among samples (but not among sections) is present in August 1978, due apparently to differences in substratum composition at the sites sampled (interpretation based on species ordinations).

During periods of copper exposure in 1978 through 1980, clear discontinuities between control and high treatment sections (7 and 15 μg l^{-1} Cu_T in 1978; 5 and 10 μg l^{-1} Cu_T in 1979–1980) exist on all sampling dates. Samples taken after two months and nine months of continuous exposure in 1979 are shown in Figs 4c and 4d, respectively. Samples of the 2.5 μg l^{-1} Cu_T section are located between control and high treatment sections on axis 1 (as in the examples presented) or with the control section samples.

Differences between control and high treatment sections persisted long after dosing (Figs 4e and 4f). Sample ordinations show clear discontinuities three months (November 1980) and eleven months (July 1981) after the year of continuous copper exposure.

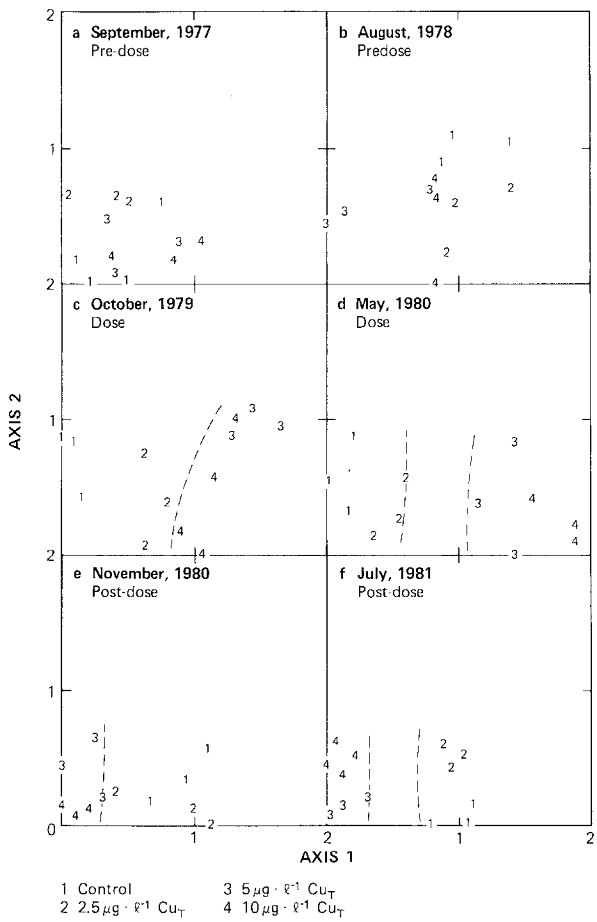

Fig. 4. Sample ordination (DCA) of population densities of aquatic insects. Axis 1 expresses either variation in biological interactions (September 1977) or substratum composition (August 1978) during the pre-dose period. During dose and post-dose periods, Axis 1 primarily expresses the sensitivity of taxa to copper (see text for details). Axis scale is average standard deviation of species turnover. Dashed lines define groups.

Species ordinations for the same pre-dose, dose and post-dose sampling periods are given in Fig. 5. A complex gradient which emphasizes biological interactions existed in June (not shown) and September 1977. In the species ordination of September samples, the principal predators, *Arctopsyche grandis, Calineuria californica, Doroneuria baumanni* and *Rhyacophila vaccua* and several herbivore-detritivores, *Baetis* spp. and *Optioservus divergens*, are located in the upper part of the diagonal gradient and most common herbivores, *Antocha monticola, Epeorus dulciana, Glossosoma* sp., *Hydroptila* sp. and *Micrasema* spp. are located towards

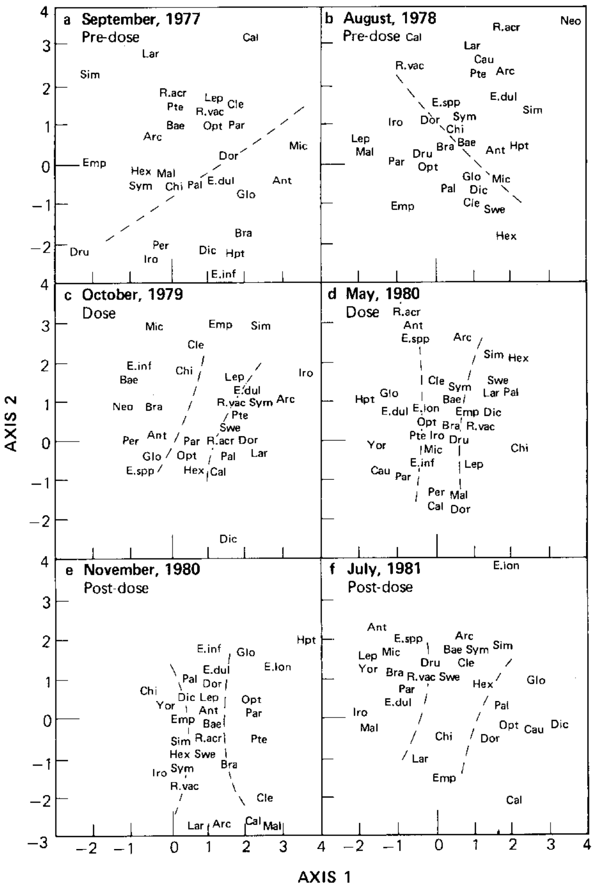

Fig. 5. Species ordination (DCA) of population densities of aquatic insects. Axis 1 expresses either variation in (a) biological interactions (September 1977) or (b) substratum composition (August 1978) during the pre-dose period. During dose (c, d) and post-dose (e, f) periods, Axis 1 primarily expresses the sensitivity of taxa to copper (see the text for details). Dashed lines define groups.

the lower part of the gradient. The August 1978 ordination emphasizes a difference in substratum composition. Taxa tolerant of sand and silt (*Lepidostoma* spp., *Paraleptophlebia pallipes, Palpomyia* spp., *Hexatoma* spp., *Dicranota* sp. and Empididae) are located in the lower left of the plot and those taxa associated with larger grain substrata are located in the upper right of the plot.

During periods of copper exposure (Figs 5c and 5d), axis 1 emphasizes the sensitivity of taxa to copper. Towards the left end of axis 1 are taxa which declined in population density at 5 to 15 $\mu g\ l^{-1}\ Cu_T$ relative to the control; towards the right end of axis 1 are taxa which did not decline in abundance at these

EPHEMEROPTERA: Bae, *Baetis* spp.; Cau, *Caudatella heterocaudata* (McDunnough); Dru, *Drunella flavilinea* (McDunnough); E. dul, *Epeorus dulciana* (McDunnough); E. lon, *Epeorus longimanus* (Eaton) E. inf, *Ephemerella infrequens* McDunnough; Iro, *Ironodes lepidus* Traver; Par, *Paraleptophlebia pallipes* (Hagen); PLECOPTERA: Cal, *Calineuria californica* (Banks); Dor, *Doroneuria baumanni* Stark and Gaufin; Mal, *Malenka* sp., probably *californica* Claassen; Pte, *Pteronarcys princeps* Banks; Swe, *Sweltsa* sp., probably *pacifica* (Banks); Yor, *Yoraperla brevis* (Banks); TRICHOPTERA: Arc, *Arctopsyche grandis* (Banks); Bra, *Brachycentrus americanus* (Banks); Glo, *Glossosoma* spp.; Hpt, *Hydroptila* spp.; Lep, *Lepidostoma* spp.; Mic, *Micrasema* sp.; Neo, *Neophylax* sp.; R. acr, *Rhyacophila acropedes* Banks; R. vac, *Rhyacophila vaccua* Milne; Sym, *Symphitopsyche oslari* (Banks); COLEOPTERA: Cle, *Cleptelmis addenda* (Fall); Lar, *Lara* sp.; Opt, *Optioservus divergens* (Le Conte); DIPTERA: Ant, *Antocha monticola* Alexander; Chi, *Chironomidae*; Dic, *Dicranota* sp.; Emp, *Empididae*; Hex, *Hexatoma* spp.; Pal, *Palpomyia* sp.; Per, *Pericoma* sp.; Sim, *Simulium* spp.

concentrations. In general, populations densities of herbivorous aquatic insects declined at 5 to 15 $\mu g\ l^{-1}\ Cu_T$, whereas population densities of predatory insects did not. Sensitivities to copper of detritivores and herbivore-detritivores varied.

Three months after dosing (November 1980), axis 1 expresses a well-defined gradient based on the sensitivity of taxa to copper (as determined during the dosing period). After eleven months (July 1981), a copper response gradient is evident, but it is complicated by the lack of recolonization of some taxa. Normal population densities of the semivoltine (two-year life cycle) *Calineuria californica, Doroneuria baumanni* and *Optioservus divergens* are not re-established in sections previously dosed at 5 or 10 $\mu g\ l^{-1}\ Cu_T$. In contrast, population densities of several univoltine taxa which hatch in autumn (*Brachycentrus americanus, Epeorus dulciana, Micrasema* sp., *Paraleptophlebia pallipes* and *Rhyacophila vaccua*) are higher in sections previously dosed at 5 or 10 $\mu g\ l^{-1} Cu_T$ than in the control.

Discussion

Ordination of species abundance data can be used to reduce redundancy, elucidate relationships among variables and identify outliers (Gauch, 1982a). It is an objective means of shifting the level of analysis from abundances of individual species to low-dimensional parameters such as species assemblages, community types and community gradients. The identification of factors controlling the spatial distribution of species is often facilitated by this shift in the level of analysis. Advantages of DCA over other ordination methods considered in this study are that direction of the primary gradient can always be determined and multispecies distributions assumed linear (Hill & Gauch, 1980).

The effectiveness of DCA in displaying the magnitude of the copper gradient is evident in the sample ordinations of 1978 and 1979 (Figs 3b and 3c). The discontinuity between the control (and low copper section) and the two higher treatment sections is greater in 1978 than in 1979, reflecting the higher levels of copper exposure in 1978. The medium and high test concentrations were 7 and 15 $\mu g\ l^{-1}\ Cu_T$ in 1978, but only 5 and 10 $\mu g\ l^{-1}\ Cu_T$ in 1979. The decrease in medium and high test concentrations in 1979 results in a lower species turnover rate (i.e. beta diversity).

Sampling of aquatic insects in Convict Creek was restricted to midstream riffle areas of visually similar substratum-particle size and similar shading and current velocities. The streambed at all sampling sites was predominantly cobbles, pebbles and coarse sand. Despite this standardization of sampling site, substratum composition appeared to be an important gradient (interpretation based on species ordinations since particle size distribution was not determined on all samples) during the pre-dose period and complicated interpretation of the copper gradient on one occasion during dosing. A complex gradient emphasizing biological interactions also was expressed during the pre-dose period. The relative importance of predation, competition and abiotic factors as controls on the abundance and distribution of aquatic insects in streams is unclear. Most investigators have emphasized the influence of physical factors such as current velocity, substratum-particle size, food and detritus (Egglishaw, 1964; Cummins & Lauff, 1969). The distribution of species in riffles is apparently controlled more by substratum than by current velocity (Minshall & Minshall, 1977), and direct velocity effects are insignificant when compared with substratum-related trapping of detritus (Rabeni & Minshall, 1977). Reice (1980) showed that many riffle insects select substrata of a specific size even when velocity differences are minimized.

An effect of substratum-particle size on species distributions was apparent in August 1978. The discontinuity between samples from sections 2, 3 and 4 (left and bottom portion of Fig. 4b) is related to the high relative abundance of taxa tolerant of sand-silt particle sizes. The particle size tolerances or preferences of some common Convict Creek taxa are listed in Table 1.

From descriptive data on spatial and temporal overlap of closely related species (Hynes, 1961; Grant & Mackay, 1969; Allan, 1975) and manipula-

Table 1. Summary of substratum and trophic preferences of common aquatic insects in Convict Creek.

Taxon	Substratum Preference	Trophic Preference	Authority
EPHEMEROPTERA			
Baetis spp.	C	H, D	Gilpin & Brusven (1970)
Baetis tricaudatus			De March (1976)
			Rabeni & Minshall (1977)
			Ward (1975)
			Allan (1975)
			Koslucher & Minshall (1973)
			Chapman & Demory (1963)
			Morihara & McCafferty (1979)
Epeorus dulciana			
Epeorus albertae (closely related to *E. dulciana*)	C	H, D	Gilpin & Brusven (1970)
			Jensen (1966)
Paraleptophlebia spp.	C, D	D	Gilpin & Brusven (1970)
			Rabeni & Minshall (1977)
			De March (1976)
			Ward (1975)
			Chapman & Demory (1963)

Taxon	Substratum Preference	Trophic Preference	Authority
PLECOPTERA			
Calineuria californica	C	P	Peckarsky (1979)
			Siegfried & Knight (1976b)
			Sheldon (1969)
Doroneuria baumanni	C	P	Stark & Gaufin (1974)
			Peckarsky (1979)
TRICHOPTERA			
Arctopsyche grandis	C	H, P	Brusven & Prather (1974)
			Hauer & Stanford (1981)
			Givens & Smith (1980)
			Alstad (1979)
			Cuffney & Minshall (1981)
Rhyacophila vaccua	C	P	Smith (1968)
Rhyacophila spp.			Thut (1969)
			De March (1976)
			Chapman & Demory (1963)
Glossosoma spp.	C	H	Rabeni & Minshall (1977)
			Chapman & Demory (1963)
			Coffman *et al.* (1971)
Hydroptila spp.	C	H	De March (1976)
			Wiggins (1977)
Lepidostoma spp.	C, F, D	D	Ward (1975)
			Wiggins (1977)
			Mackay & Kalff (1969)
			Chapman & Demory (1963)
			Anderson & Cummins (1979)
Micrasema spp.	C, F, V	H	Ward (1975)
			Wiggins (1977)
			Chapman & Demory (1963)
COLEOPTERA			
Optioservus divergens	C, F	H, D	Koslucher & Minshall (1973)
Optioservus spp.			Chapman & Demory (1963)
			Coffman *et al.* (1971)
			Rabeni & Minshall (1977)
			Le Sage & Harper (1976)
			Brown & White (1978)
			Godbout & Hynes (1982)
DIPTERA			
Dicranota sp.	F	P	Merritt & Cummins (1978)
			Godbout & Hynes (1982)
Antocha spp.	C	H	Godbout & Hynes (1982)
			Coffman *et al.* (1971)
			Merritt & Cummins (1978)
			Johannsen (1934)
Palpomyia sp.	F, C	D, P	Ward (1975)
			Coffman *et al.* (1971)
			Merritt and Cummins (1978)
Hexatoma spp.	F	D, P	Ward (1975)
			Mackay & Kalf (1969)
			Coffman *et al.* (1971)
			Johannsen (1934)
Empididae	C, F	P	Merritt & Cummins (1978)
			Ward (1975)

Substrate Preference:
C = gravel or larger; F = sand or smaller; D = detrital accumulations; V = vegetation.
Trophic Preference:
H = herbivore; D = detritivore; P = predator.

tive experiments, several investigators have concluded that competition is also an important determinant of community structure. Manipulative experiments, in which physical factors are held constant and competitive interactions are examined, indicate that exploitative competition occurs among stream herbivores (McAuliffe, 1985; Hart, 1981) and detritivores (Nilsson & Otto, 1977). Wiley (1981) showed that competition influences spatial distributions of chironomid larvae. Additional evidence that competitive interactions play an important role in the organization of stream communities was presented by Hart (1983). In contrast, Reice (1981) argued that the intense predation pressure, abundant food resources and frequent disturbances of many streams combine to minimize the role of competition.

Predator-prey interactions also influence the abundance and distribution of benthic insects (Hildrew & Townsend, 1980; Siegfried & Knight, 1976a). Food resources may not be the primary factor affecting distribution of predators (Peckarsky & Dodson, 1980b). Physical habitat cues and mutual interference among predators have been identified as factors limiting predator-prey interactions in streams (Peckarsky & Dodson, 1980a; Wiley & Kohler, 1981).

In this study, we did not experimentally investigate specific responses of individual taxa to predation, competition or food availability. Nevertheless, the ordination (DCA) used to summarize spatial distributions of species displayed species-specific responses to biotic and abiotic gradients. During the pre-dose period, the species ordinations displayed gradients emphasizing either biological interactions or substratum composition. Once dosing began, the species ordinations indicated a complex gradient of two related factors. A sensitivity to copper was expressed by the ordering of taxa relative to their abundances in each section, i.e. their relative abundances declined as the copper concentration increased across sections. In addition, the gradient expressed an ordering based on food preference, with abundances of herbivorous taxa declining more than predators or detritivores as copper concentration increased. Prior to the post-dose sampling of July 1981, a one-month period of streambed scouring due to high discharge occurred. This disturbance caused both total density (individuals $\cdot$ m^{-2}) and total biomass (weight $\cdot$ m^{-2}) of aquatic insects to decline markedly and created similar levels of these characteristics in all sections. DCA continued to show a strong discontinuity between the control (and low copper section) and the medium and high dosed sections. The factor apparently responsible for a discontinuity persisting eleven months after dosing was the lack of recolonization of semivoltine taxa in the medium and high dosed sections. In contrast, several univoltine taxa which hatch in autumn were more abundant in the medium and high dosed sections than in the control.

Devising a direct method of evaluating the relative importance of abiotic factors, competition and predation in structuring a given benthic insect community has proved difficult. Although the most informative approach may involve the experimental manipulation of insect densities (Hart, 1984), these manipulations are not generally practical in water pollution investigations. The lack of time and entomological expertise of field personnel frequently dictate a more descriptive approach. Ordination by DCA does not permit hypothesis testing but it does effectively display major gradients affecting the spatial distribution of species. The method may therefore prove useful in future studies of microdistribution of benthic invertebrate communities.

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