ORDINATION OF DEEP RIVER INVERTEBRATE COMMUNITIES IN RELATION TO ENVIRONMENTAL VARIABLES

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Abstract

A deep Main river was examined to determine the effects of selected environmental variables on benthic invertebrate community structure. Thirty-three sites were sampled by divers using artificial substrates. The Bray-Curtis ordination was used to establish community types based upon combinations of current velocity, siltation, and organic detritus. While some invertebrates were tightly clustered within particular communities, most taxa tended to concentrate in one community type but were not excluded from others. The results tended to support the individualistic hypothesis of species distribution.

Introduction

The principles of lotic invertebrate ecology have been developed primarily from the study of easily accessible streams. Problems associated with sampling the fauna of deep, moderate to fast flowing rivers have limited the information available on this type of habitat. Only recently have advances in techniques used by divers allowed consistently reliable samples from deep river bottoms with rubble substrates to be obtained (Gale & Thompson, 1974a, 1974b; Rabeni & Gibbs, 1978).

The objective of this study was to determine the effect of several environmental variables on invertebrate distribution in a deep Maine river and to examine how community structure changes along environmental gradients. To determine how benthic invertebrate communities varied among the sites, a community ordination technique was used. This method of analysis was chosen because it compares the actual species composition while other methods, such as diversity indices, compare only the number of taxa and individuals in a community, regardless of what the actual species are. Ordination techniques also allow an evaluation of the environmental factors influencing the differences between communities.

Studies which have isolated important controlling environmental variables in more shallow, smaller streams suggested factors to investigate in this study. All of the following have been shown to be important: water velocity, water temperature, water chemistry, oxygen, siltation, and detritus. Substratum type is of major importance but has been standarized and eliminated as a variable in this study.

Methods and materials

The Penobscot River watershed drains approximately 25% of the State of Maine. The study area consisted of 100 km stretch of the main river and two tributaries between Grindstone and Old Town, Maine. Discharges at Enfield, approximately midway in the study area, have a 73 year average of 332 m^3/s and ranged from 1,345 m^3/s to 119 m^3/s during the year of the study (Anon., 1976). Thirty-three sites offering a range of depths and water velocities were chosen throughout the study area. When artificial substrates were set in place current velocities ranged from 10-50 cm/sec and water depths ranged from 0.6-5 m. Commercially available wire baskets were filled with stones of a uniform size (construction grade 2½ in.) and placed by divers on the bottom of the river. They were left in position for approximately four weeks. Substrates were retrieved by a diver who swam up to a basket from downstream and held a fine mesh collection bag directly behind it. The basket was carefully lifted, placed into the collection bag, brought to the surface and placed in the boat. The stones were then cleaned and the washings were concentrated through a # 30 mesh screen (600 μ openings)

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and preserved in 5 percent formalin. The artificial substrates are similar to those used in water quality studies by Anderson & Mason (1968), Dickson *et al.* (1971), Mason *et al.* (1971), Benfield *et al.* (1974), and is a method recommended by the United States Environmental Protection Agency (Weber, 1973). The baskets have been shown to be somewhat selective in the types of organisms that colonize them but they do have the advantages of eliminating the substratum variable, collecting large numbers of organisms and making sites more comparable.

The variation among replicate samples in nonpolluted sites in this river was low. The coefficient of variation was 15.3% for the number of taxa and 20.0% for the number of individuals (Rabeni & Gibbs, 1978). This may be due to the relatively homogeneous habitat of the deep river. Factors affecting the microdistribution of benthic invertebrates are more uniform at the substratum of a deep river than in a smaller stream. Using the method of Elliott (1971) we determined that two replicates would usually suffice to be within 20% of the true mean for the number of taxa and for the number of total individuals. Current velocities were measured near the front of the baskets before retrieval and pH, temperature, and oxygen readings were taken at the water surface and near the substratum. Transparency, turbidity, alkalinity, total hardness and water depth were measured at each site. Organic detritus from each artificial substrate was air dried and weighed.

To determine the amounts of siltation that accumulated during the colonization period, one basket from each site was retrieved by a diver using a rigid plastic pail with a lid. Once in the boat the entire contents, rocks and water, were transferred to a large tub and the tub filled to a predetermined point with water. The contents of the tub were well swirled and a 500 ml sample was removed. This water was later filtered through a glass fiber filter to determine total suspended solids (American Public Health Association, 1973). These results were used as an indication of the relative amounts of siltation that occurred at each site.

Benthic Invertebrate Ordination

The Bray & Curtis (1957) method used here was one of the first and simplest measures of ordination but has been shown to be one of the most effective (Beals, 1972; Gauch & Whittaker, 1972).

This technique involves the determination of the degree of similarity for community pairs (sampling sites) by calculating a set of community similarity coefficients, and the arrangement of the benthic communities on a two axis system on the basis of differences in composition as expressed by the community similarity coefficients (Bray & Curtis, 1957). The method chosen for determining similarity coefficients was one termed percentage similarity and the set of community similarity coefficients (PS) was calculated according to the equation given by Gauch & Whittaker (1972):

$$PS = 2\frac{\Sigma \min (P_{ij}, \quad P_{ik})}{\Sigma \quad (P_{ij} + P_{ik})}$$

where P_{ij} and P_{ik} are the percentage of organisms of species i in communities j and k.

The value of (PS) may range from 0 for communties having no species in common to 1 for two communities identical both in species composition and in percentage values for each species. The calculated similarity measure was then subtracted from a constant (1.00) to produce the dissimilarity distance measurement which was needed for the ordination.

Ecologically dissimilar sites were chosen as end points on the X axis and the other communities were positioned in relation to them. End points on the Y axis were chosen from those ecologically dissimilar sites near the center of the X axis and again the rest of the communities were positioned relative to these. (See Beals (1960) for the formulae). A Cornell Ecology Program modified for the University of Maine's computer was used.

The distance between plotted points (communities) may be thought of as an ecological distance where the more alike communities are grouped closest together. Once the ordination is complete, it may be used to evaluate environmental factors affecting benthic community composition.

Results and discussion

Interpretation of Axes

The ordination was first examined for relationships between plotted communities and environmental variables. Coordinates for all 33 sampling stations are given in Fig. 1. Fig. 1A shows the separation of communities based upon current velocity at the time of substrate removal. The upper left portion of the ordination contains a majority of communities with current velocities above 11 cm/sec. Sites in the central portion of the ordination averaged between 5-11 cm/sec and the lower right 19 communities are predominately those with a current velocity less than 5 cm/sec.

The relative siltation effect is found to correspond rather well to the distribution of communties based upon current

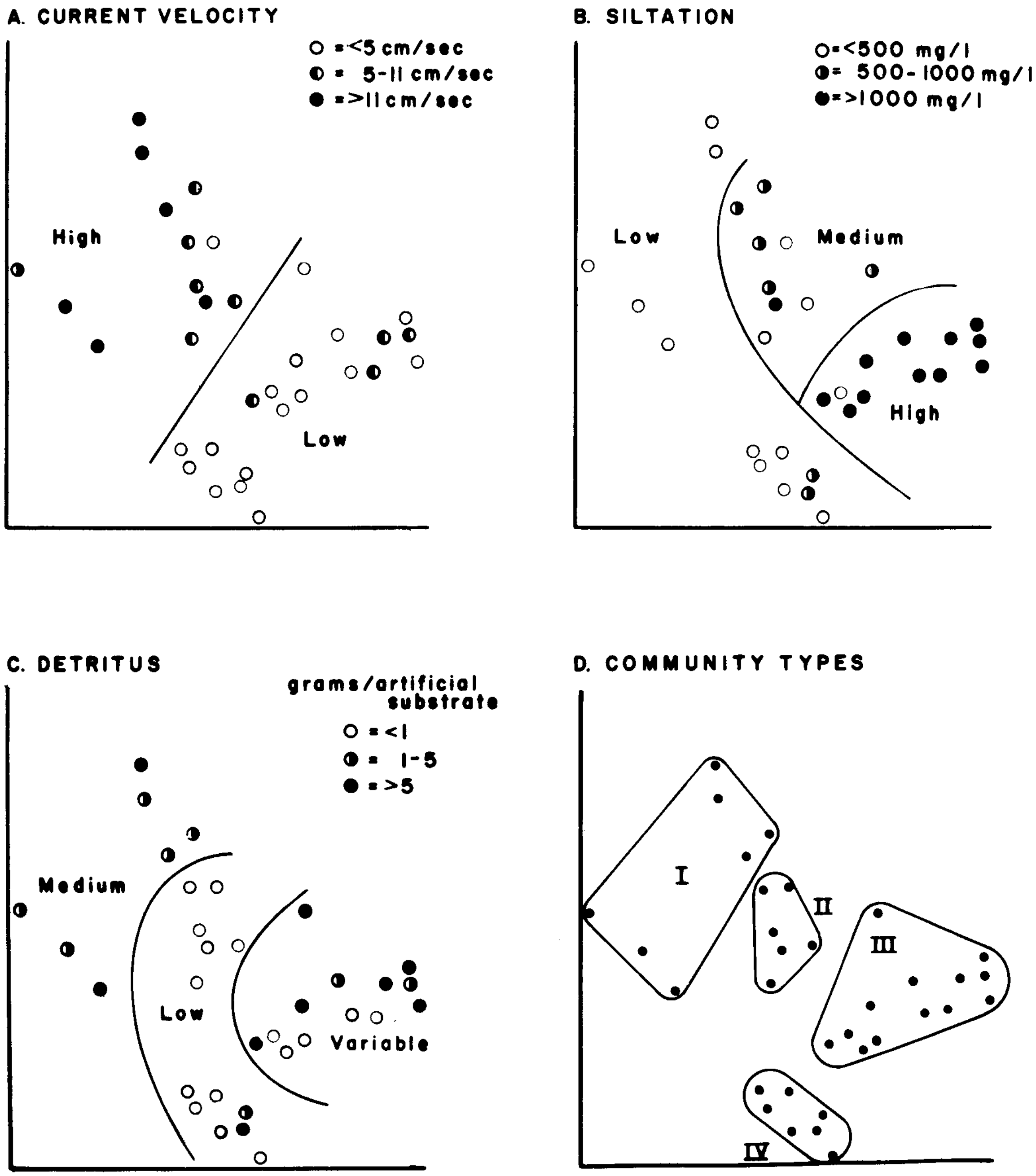

Fig. 1. An ordination of invertebrate communities showing the distribution of environmental factors and the four community types.

velocity (Fig. 1B). This is to be expected as the two parameters are directly related and normally higher levels of siltation occur at lower current velocities. Seven communities are grouped together in the lower center of the ordination which show low current velocities yet low siltations. This apparent contradiction may be because these stations are all from river sections which have consistently shown the lowest turbidity readings and the highest transparency measurements. It may be that when the current slowed there was just little or no silt to settle out.

The distribution of communities in relation to detritus (i.e., leaves, grasses and other potential invertebrate food) tended to clump, but not in a gradient from low in one end of the ordination to high in the other (Fig. 1C). Communities containing low detrital amounts are found in the center of the ordination and medium detritus communities are those in the upper left portion. The right portion of the ordination contains communities with detrital amounts varying from low to high.

There was little or no clumping based upon water depths or water turbidity. Several other parameters, including water temperature, dissolved oxygen, pH, alkalinity, water hardness, and conductivity, were examined. None varied sufficiently among sites to indicate a general gradient on the ordination and they can be assumed to have little effect on organism distribution.

Four community types were distinguished from the distribution of communities in relation to those environmental factors which showed a pattern on the ordination (Fig. 1D): I. high current, low silt, medium detritus; II. medium current, medium silt, low detritus; III. low current, high silt, variable detritus; IV. low current, low silt, low detritus. Communities I, II, and III on the ordination represent clear gradients of current velocity and siltation and less of a gradient of detritus (Fig. 1).

Distribution of Individual Taxa

Once the main environmental factors influencing community structure were defined, the taxa were examined to determine how they corresponded to the established community types. The majority of taxa predominated in one community type (either I or III) while fewer taxa predominated in community types II and IV.

The greatest number of taxa concentrated in community I (Fig. 2 and Table 1a). Four were net-spinning or seine weaving caddisflies whose food gathering technique depends upon a moderate current to deliver food, and in the case of *Neureclipsis* and *Chimarra,* to keep the nets open. *Brachycentrus numerosus,* a wood case building caddisfly, is typically found in shallow, fast-flowing streams where it is cemented to the upper surface of rocks and debris in the main force of the current. Two baetid mayflies, *Baetis* and *Isonychia,* known for their high oxygen requirements (Ambuhl, 1959), were concentrated in this community. The Diptera which predominated in this area were two Chironomidae, *Conchapelopia* and *Polypedilium.*

Community II possessed an intermediate environment between communities I and III and it contained relatively few predominant taxa (Table 1b). Important in this community were three species of mayflies, a riffle beetle and a snail.

Community III contained concentrations of most of the non-insect invertebrates: oligochaetes, the fingernail clam *Musculium,* the isopod *Asellus* and the leech *Helobdella stagnalis* (Fig. 3 and Table 1c). Also predominant here were the mayflies *Paraleptophlebia volitans* and *Stenonema interpunctatum* and two seine building caddisflies, *Nyctiophylax* and *Polycentropus.*

Only two taxa, the stonefly *Acroneuria abnormis* and the dragonfly *Boyeria grafiana,* predominated in community IV. Several taxa concentrated in one community but extended their range into an adjacent one while a fewer number did not concentrate in any of the communities (Table 1 and Fig. 4). This may indicate a wide tolerance to the environmental variables that were measured.

Environmental Influence

The ordination was used in order to examine the responses of organisms to a multiplicity of environmental factors and it is concluded that invertebrate community structure of this deep river is affected by interactions of current velocity, siltation, and detritus. Current velocity is probably the overriding factor because it affects the other two variables (Rabeni & Minshall, 1977). Adequate current is the controlling factor in community I and II and lack of current causing siltation appeared to be most responsible for the structure of community III. The fact that few taxa predominated in community IV and that it possessed low values of the three environmental parameters strengthens the conclusion of the importance of these factors in determining structure of the other community types. The influence of detritus in this situation is less clear. Its importance in the high silt community may have been overlooked because many of the inhabitants may utilize silt size organic particles which were not measured. Its importance in communities I and II, more typical riffle assemblages, cannot be separated from current as they both decrease from the highly populated community I to the lesser populated community II.

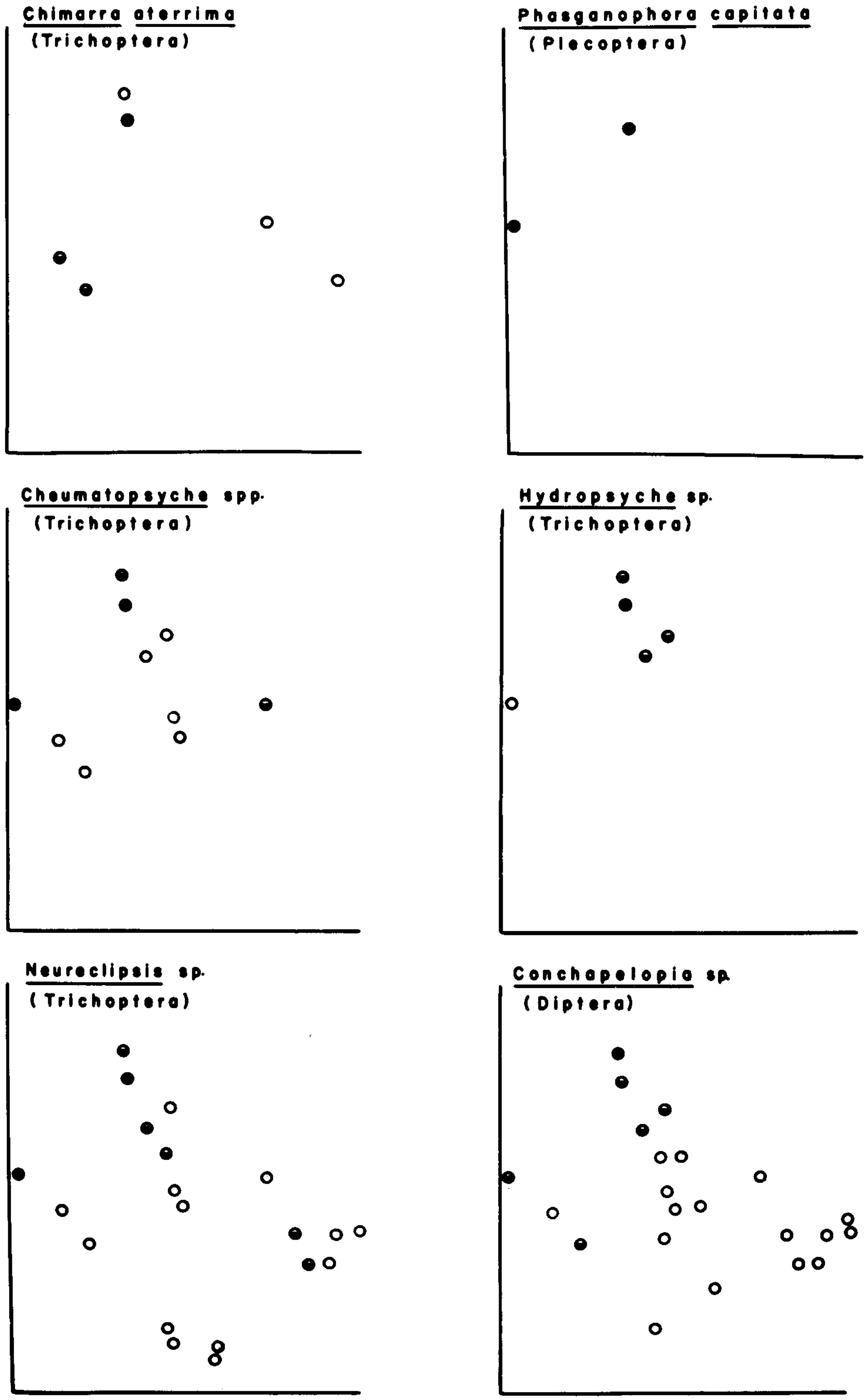

Fig. 2. The percentage distribution of representative taxa concentrating in community type I. Open circles equal 1-10%, half filled circles are 11-25%, full circles are over 25%.

Table 1. Distribution of individual taxa among the four community types. Values are percentages of the total and have been weighted to compensate for unequal numbers of sampling stations of the communities. The numbers in parentheses after the taxa are total numbers collected. Percentages may not equal 100 because values less than one at any one station were disregarded.

	Community Type 1	2	3	4
(a) Distribution concentrated in community type I				
Brachycentrus numerosus (32) (Trichoptera)	100.0	0	0	0
Phasganophora capitata (11) (Plecoptera)	100.0	0	0	0
Helicopsyche borealis (47) (Trichoptera)	98.9	0	1.0	0
Ephemerella temporalis (36) (Ephemeroptera)	97.2	0	0	2.7
Ephemerella deficians (52) (Ephemeroptera)	97.0	0	1.0	1.9
Chimarra aterrima (345) (Trichoptera)	97.0	0	2.9	0
Hydropsyche sp. (282) (Trichoptera)	96.1	2.3	0	1.0
Isonychia sp. (71) (Ephemeroptera)	95.6	0	1.5	2.8
Cheumatopsyche sp. (1480) (Trichoptera)	89.6	7.0	3.2	0
Ithytrichia sp. (25) (Trichoptera)	88.5	9.3	2.1	0
Stenonema fuscum (19) (Ephemeroptera)	79.0	0	0	2.0
Baetis sp. (71) (Ephemeroptera)	76.3	18.3	3.8	1.4
Cryptochironomus sp. (31) (Diptera)	72.0	0	27.9	0
Simulium sp. (31) (Diptera)	68.1	30.0	1.7	0
Conchapelopia sp. (272) (Diptera)	67.7	15.9	16.2	0
Neureclipsis sp. (106) (Trichoptera)	63.8	13.1	13.9	9.1
Acroneuria lycorias (271) (Plecoptera)	59.9	31.9	8.0	0
Neurocordulia sp. (30) (Odonata)	59.9	13.1	8.0	18.7
Ephemerella invaria (Ephemeroptera)	50.0	49.9	0	0
Physa sp. (86) (Mollusca)	52.5	26.8	15.7	4.9
Stenonema ithaca (34) (Ephemeroptera)	48.4	9.8	4.5	37.0
Erpobdella punctata (39) (Hirudinea)	46.2	15.1	38.6	0
Centroptilum sp. (171) (Ephemeroptera)	45.2	33.4	18.2	3.0
Microtendipes sp. (1112) (Diptera)	40.9	27.9	21.5	9.5
Oecetis sp. (53) (Trichoptera)	34.3	24.1	29.8	11.6
(b) Distribution concentrated in community type II				
Ephemerella walkeri (7) (Ephemeroptera)	25.0	74.0	0	0
Amnicola sp. (334) (Plecypoda)	0	62.9	27.2	9.7
Stenonema smithae (678) (Ephemeroptera)	23.3	51.5	23.7	1.7
Planariidae (40) (Annelida)	15.3	47.5	37.1	0
Ephemerella attenuata (204) (Ephemeroptera)	39.7	40.5	10.7	8.9
Stenelmis crenata (253) (Coleoptera)	36.6	38.7	11.0	13.5
Tricorythodes sp. (284) (Ephemeroptera)	28.4	37.3	34.1	0
(c) Distribution concentrated in community type III				
Ephemerella bicolor (3) (Ephemeroptera)	0	0	100.0	0
Tubificidae (50) (Annelida)	0	0	96.1	3.9
Musculium sp. (2216) (Mollusca)	8.0	7.6	87.4	0
Helobdella stagnalis (118) (Hirudinea)	3.6	10.6	85.7	0
Asellus sp. (101) (Isopoda)	33.5	13.4	52.9	0
Hyalella azteca (396) (Amphipoda)	13.3	34.9	51.7	0
Stenonema interpunctatum (144) (Ephemeroptera)	0	9.1	48.7	42.1
Leptophlebia nervosa (76) (Ephemeroptera)	7.0	43.3	47.8	1.7
Paraleptophlebia volitans (683) (Ephemeroptera)	7.2	30.6	46.7	15.3
Nyctiophylax sp. A. (77) (Trichoptera)	0	16.3	43.4	40.2
Polycentropus sp. (367) (Trichoptera)	17.1	30.6	36.2	15.8
(d) Distribution concentrated in community type IV				
Boyeria grafiana (22) (Odonata)	15.1	17.6	21.6	45.1
Acroneuria abnormis (55) (Plecoptera)	26.3	21.5	6.9	45.0
(e) Distribution not concentrated in any one community type				
Heptagenia sp. (454) (Ephemeroptera)	26.1	22.9	22.0	28.9
Tanytarsus sp. (93) (Diptera)	35.2	9.9	17.0	37.8
Ablabesmyia sp. (316) (Diptera)	35.6	32.9	26.6	4.8
Gomphus sp. (40) (Odonata)	31.8	29.6	32.7	5.8

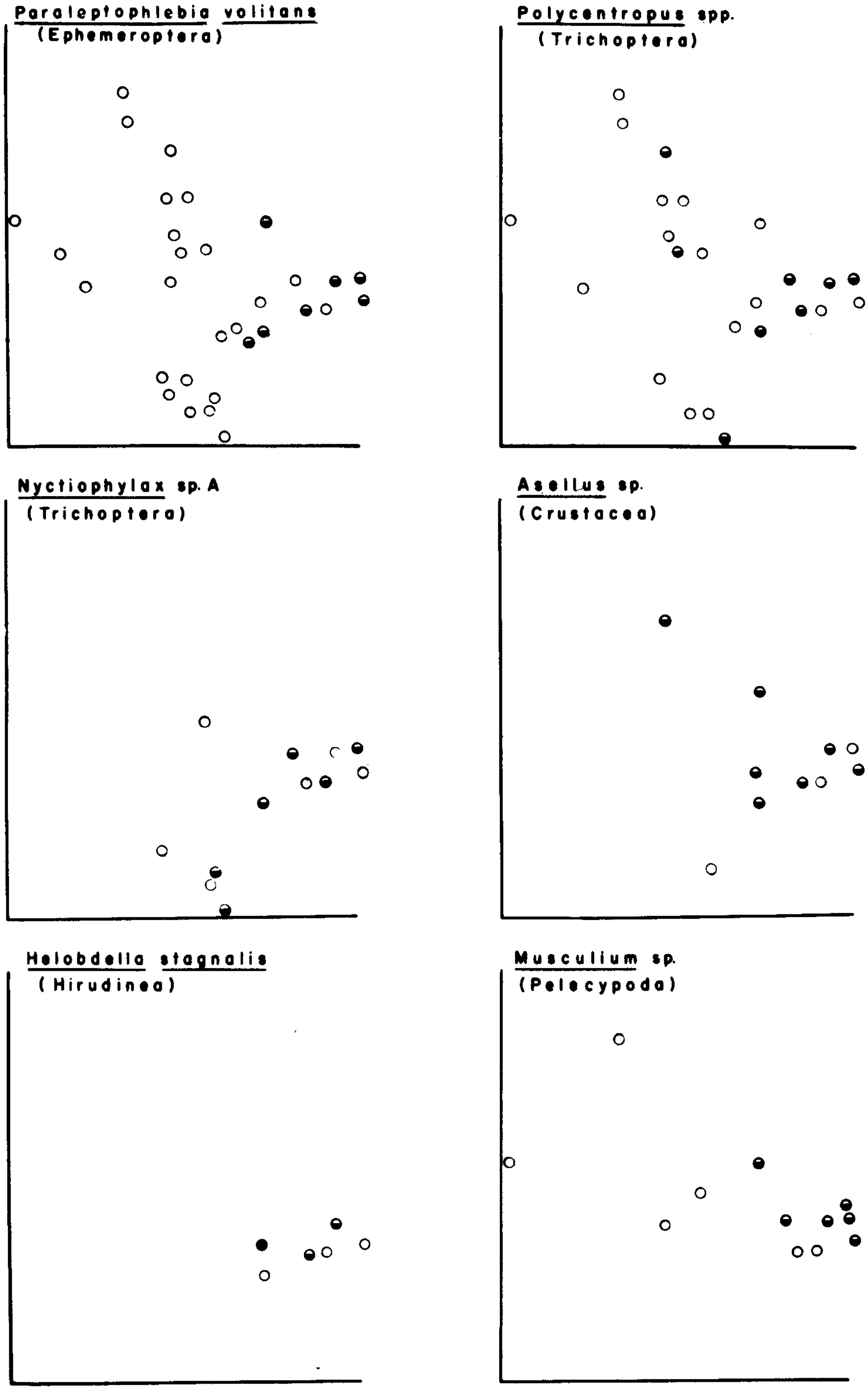

Fig. 3. The percentage distribution of representative taxa concentrating in community type III. Open circles equal 1-10%, half filled circles are 11-25%, full circles are over 25%.

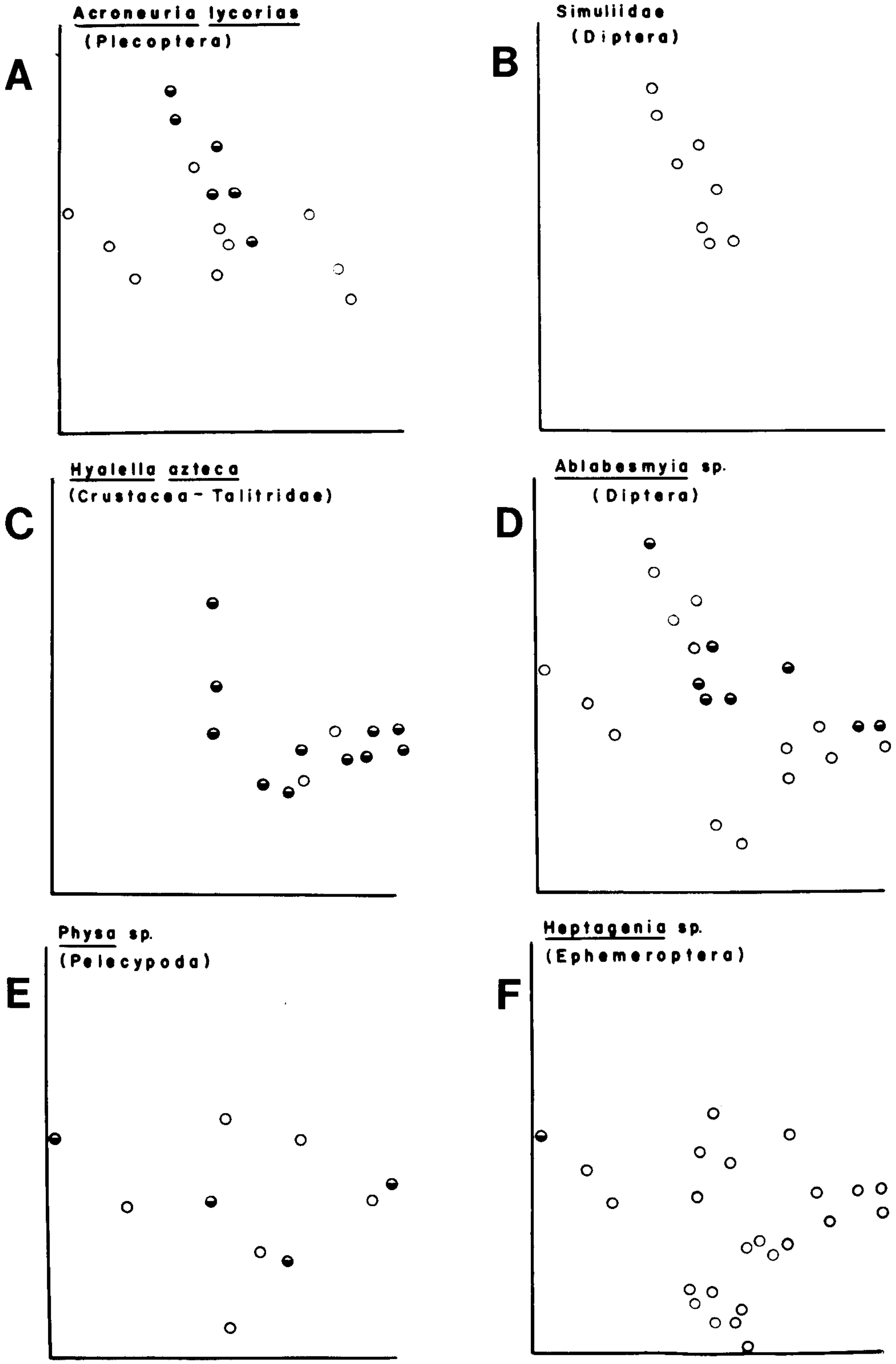

Fig. 4. Percentage distribution of representative taxa concentrating in community types I and II (A, B), II and III (C, D), and taxa which do not concentrate in any particular community type (E, F). Open circles equal 1-10%, half filled circles are 11-25%, full circles are over 25%.

Environmental Gradient

The question of how species populations develop in response to environmental gradients has been extensively debated in the botanical literature (see Whittaker, 1967 for a review) but has been seldom applied to animal populations (Whittaker, 1962) and never to deep river invertebrates. The question, as stated by Whittaker is: are communities well defined natural units which contact one another along rather narrow boundaries or do communities which occur along continuous environmental gradients intergrade continuously with gradual changes in population levels of species along the gradient? These two approaches have been respectively named the 'community unit' theory and the 'individualistic hypothesis'. The gradients of current velocity and siltation between communities I, II, and III provide an opportunity to examine this question for deep river invertebrates. This information has particular relevance for pollution biology in that if in fact a typical pollution community with well developed species boundaries exists it would certainly facilitate the use of community structure in water quality classification schemes.

Results of this study indicate that, while some invertebrates were tightly clustered within the arbitrary community types, most taxa tended to concentrate in a particular community type but were not excluded from others. For example, *Phasganophora capitata, Hydropsyche, Cheumatopsyche* and *Chimarra aterrima* are clustered almost exclusively in community I while *Neureclipsis, Conchapelopia, Acroneuria lycorias,* and the Simuliidae have a majority of their numbers in community I but tend to expand their ranges into community II. *Helobdella stagnalis, Musculium,* and *Asellus,* are tightly clumped in community III. Others, such as *Paraleptophlebia volitans, Polycentropus, Hyalella azteca,* and *Ablabesmyia* predominate in community III but are found in moderate numbers in community II. Community II appears to be an ecotone into which the community types I and III intergrade. Dispersion patterns would therefore appear to support the individualistic hypothesis. Community types can be distinguished from continuously changing species populations however, especially if relative abundances are used. As one moves from community I to III there are shifts in the dominance of certain taxa as well as the introduction of some and the elimination of others. The community types established on the basis of environmental factors (Fig. 1) are shown to have typical and distinguishable associated biota.

Summary

The benthic invertebrate fauna of a deep Maine river was sampled by divers using artificial substrates. Thirty-three sites represented a variety of habitat conditions.

The Bray-Curtis ordination was used to examine the influence of several environmental variables on community structure and on the distribution of individual taxa.

The distribution of taxa within the river appeared to be most influenced by current velocity and siltation and to a lesser extent by organic detritus. Four community types were distinguished from the distribution of the samples on the ordination in relation to the environmental variables.

While some taxa were collected exclusively within one of the arbitrary community types, most taxa concentrated in a particular community type but were not excluded from others. This pattern of distribution tended to support the 'individualistic hypothesis' of species distribution in relation to environmental gradients.

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