INERTIA AND RECOVERY: AN APPROACH TO STREAM CLASSIFICATION AND STRESS EVALUATION[1]

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ABSTRACT: The concepts of inertia and elasticity were applied to existing fish data from Conowingo Creek. It was determined that these two concepts could form the foundation for a stream classification system based on the structure and function of fish communities. Inertia appears to be more useful for predicting the effects of potential stress than elasticity (a stress must first occur before elasticity can be fully evaluated). The relationship between structural and functional redundancy and their influences on the inertia index is discussed.
(KEY TERMS: recovery; inertia; elasticity; stress evaluation; structural and functional redundancy.)

INTRODUCTION

The assessment of ecosystems has evolved from the presentation of flora and fauna lists to a series of classification schemes which include: species-area curves (Gleason, 1922), diversity indices (Shannon and Weaver, 1949; Margalef, 1958; Wilhm and Dorris, 1968; Cairns, *et al.,* 1968; among others), autotrophic-heterotrophic ratios (Weber, 1973), saprobian designations (Bick, 1958; Cairns, 1977), and biotic indices (Weber, 1973). Ott (1978) summarized water quality indices which are presently being used throughout the United States, and suggested that one approach is the development of "specific-use indices." Additionally, lotic habitats have been classified on the basis of calcium content (Ohle, 1937), distribution of fauna (Smith, 1971; Thompson and Hunt, 1930), water zones (Illies, 1961), gradient (Trautman, 1942), and stream order (Kuhne, 1962). However, Platts (1974) suggested that these classification systems had limited value to the management of land and water systems.

A more useful technique would center on parameters which could predict the amount of stress a particular system could assimilate and the potential of a system to recover once a structural or functional change of the biota was effected. The concepts of inertia and elasticity (Cairns and Dickson, 1977) appear to have great potential for use in a water resource classification system, as well as strong management implications. The purpose of this study is to examine the feasibility of using a system based on inertia and elasticity and to apply these concepts to data collected by Hocutt and Stauffer (1975) on Conowingo Creek.

METHODS AND MATERIALS

Data on the occurrence and distribution of fishes used for the calculation of inertia and elasticity indices were obtained from Hocutt and Stauffer (1975). Fishes were collected using seines and electroshocking techniques at eleven stations along Conowingo Creek (Figure 1). Hocutt and Stauffer (1975) calculated diversity indices using the Brillouin formula:

$$H = \frac{1}{N} \times \log_e \left(\frac{N!}{N_1! \times N_2! \times \ldots \times N_S!} \right)$$

where N is the number of organisms in the collection; N_1, N_2, N_i are the number of organisms in species one, two, ... etc.; and S is the number of species in the collection (Pielou, 1977).

For the purposes of this study, Conowingo Creek was divided into four sections based on stream order and gradient. Stream Section I includes Stations 1, 2, and 3 (Stream Order 1); Section II includes Stations 4 and 5 (Stream Order 2; gradient between 5 and 10 m/km); Section III includes Stations 6, 7, 8, and 9 (Stream Order 3; gradient between 2 and 5 m/km); and Section IV includes Stations 9 and 10 (Stream Order 3; gradient greater than 25 m/km) (Table 1; Figure 1).

Data from Conowingo Creek were also plotted using ordination theory as described below (Hocutt, 1975). Mean number of individuals and mean number species were calculated using data from all stations; these values formed the vectors between the quadrants. Data from each station were then plotted and analyzed respective to the quadrant into which they fell (Figure 2). The exact methods used for calculating both inertia and elasticity indices are described below.

CALCULATIONS OF INERTIA INDICES

Cairns and Dickson (1977) define inertia as the capacity of a stream to withstand a particular stress without eliciting a structural or functional change. They further state that the inertia of the system is based on the following parameters: (A) whether or not the indigenous organisms are accustomed to highly variable environmental conditions; (B) the structural
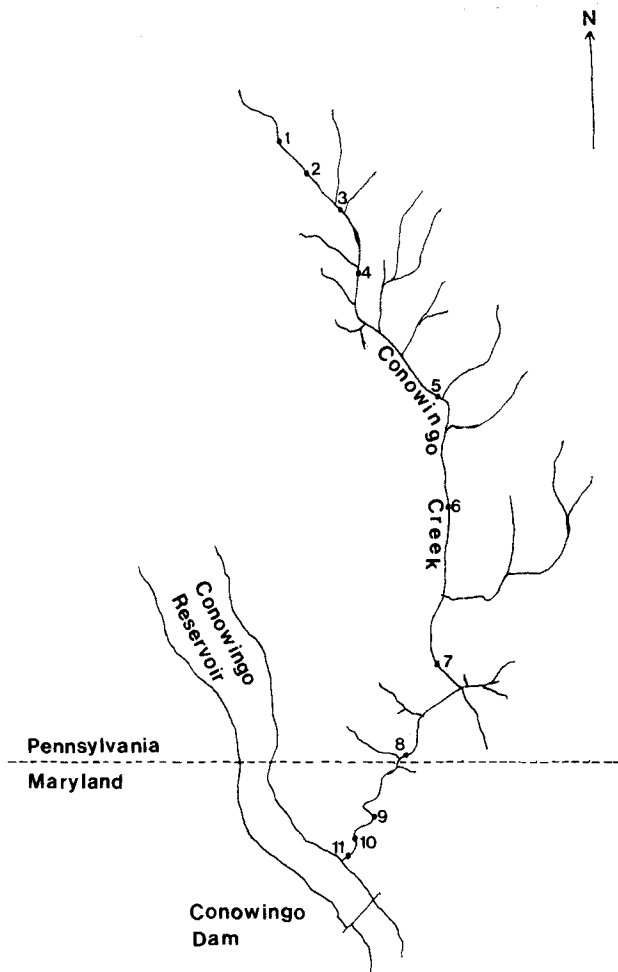
Figure 1. Map of Conowingo Creek
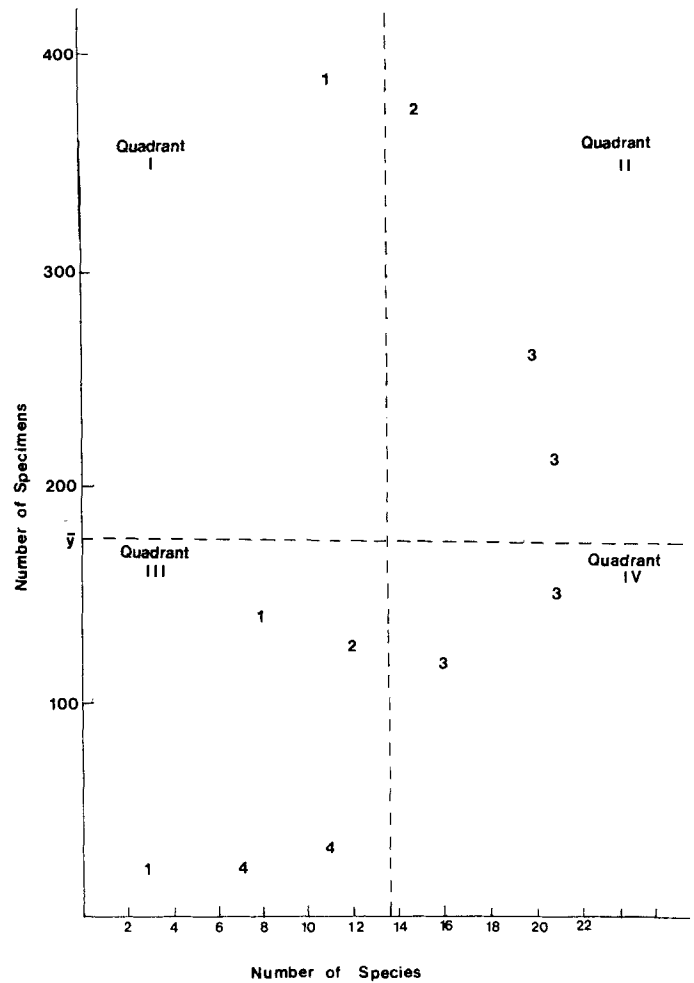(Hocutt and Stauffer, 1975).

Figure 2. Number of Specimens Versus Number of Species
for Stations in Each Stream Section of Conowingo Creek.

and functional redundancy of the stream; (C) stream order, flow dependability, flushing capacity, etc.; (D) the presence of well-buffered water antagonistic to toxic substances; (E) how close the system is to a major ecological transitional threshold; and (F) the presence of a drainage basin management group with a water quality monitoring program.

Each of the parameters which were hypothesized to influence inertia, were rated using a three-point scale (1 = poor, 2 = moderate, and 3 = good) for each of the stream stations, and an inertia index calculated: Inertia Index = A x B x C x D x E x F (Cairns and Dickson, 1977).

Using the above system, a value of 2 was assigned to Category A for each stream section, since streams in general have higher variable environmental conditions than ocean systems, but much less variable conditions that estuarine or tidal environments. Theoretically, this variable may have been omitted from the comparisons since it was the same for all four sections; however, in order to make a rough approximation with the ranges suggested by Cairns and Dickson (1977), it must be retained.

Category B is an evaluation of the structural and functional redundancy of the system. Structural redundancy was

estimated using the four families which were represented by more than one species (Table 1): Cyprinidae (genera: *Campostoma, Clinostomus, Exoglossum, Nocomis, Notropis, Pimephales, Rhinichthys,* and *Semotilus*); Catostomidae (genera: *Catostomus* and *Hypentelium*); Ictaluridae (genera: *Ictalurus* and *Noturus*); and Centrarchidae (genera: *Lepomis* and *Micropterus*). The number of species in a particular stream section was divided by the total number of species from that family present in the Conowingo Creek drainage (Table 2). For example, in Section I, there were 7 of 15 species present from the Cyprinidae, 2 of 2 from Catostomidae, 0 of 3 from Ictaluridae, and 0 of 4 from Centrarchidae. The mean structural redundancy from Section I was 0.367.

For the purposes of this paper, functional redundancy was evaluated using only trophic level interactions (Table 1) based on food studies described in Carlander (1969), Scott and Crossman (1973) and our general knowledge of food habits for these species. It was determined that 18 species interacted at Trophic Level I, 26 at Level II, 22 at III, 10 at IV, and 2 at V (Table 3). Functional redundancy values were tabulated using a method similar to that for structural redundancy. It should be noted that many fish interacted at more than one

TABLE 1. Fishes Collected From Conowingo Creek (Hocutt and Stauffer, 1975), Grouped by Stream Section (trophic levels at which each species intersects are indicated).

Stream Section	I			II		III				IV			Trophic Level			
Station	1	2	3	4	5	6	7	8	9	10	11					
Gradient (m/km)	19.3	10.0	13.4	7.8	5.5	3.0	3.0	2.5	3.4	28.4	28.4					
Stream Order	1	1	1	2	2	3	3	3	3	3	3					
Number of Species	3	8	11	15	12	21	20	21	16	7	11	I	II	III	IV	V
Brillouin Diversity Index	0.58	0.73	1.72	1.78	1.98	2.31	2.53	2.23	2.10	1.11	1.68					
Anguilla rostrata			3	1					1					X	X	X
Salmo trutta						1							X	X	X	
Campostoma anomalum			1	8	8	19	25	2	7			X	X			
Clinostomus funduloides		3	51	13	18	2	1						X	X		
Exoglossum maxillingua	1	3	35	39	7	20	7	17	7	1			X	X		
Nocomis micropogon				1	1	1	2	4	11	12	10	X	X	X		
Notropis analostanus							23	1	20			X	X	X		
Notropis cornutus		1	18	18	30	26	6	13	25	4	1	X	X	X		
Notropis hudsonius				1	7	19	38	9	5		1	X	X	X		
Notropis procne						3	24	8	1			X	X	X		
Notropis rubellus							1	1	14	1	1	X	X	X		
Notropis spilopterus						2	14	11			4	X	X	X		
Pimephales notatus							6	74	1			X	X			
Rhinichthys atratulus	17	110	178	168	24	15	22	1	6		1	X	X			
Rhinichthys cataractae		5	17	15	11	8	13	8	1		2	X	X	X		
Semotilus atromaculatus	5	8	30	44	11	8	1	3				X	X	X	X	
Semotilus corporalis						1						X	X	X	X	
Catostomus commersoni		3	25	14	1	3	21	18	13	2	3	X	X			
Hypentelium nigricans			12	9	4	7	10	3	2			X	X			
Ictalurus nebulosus						1						X	X	X	X	
Ictalurus punctatus										1	4	X	X	X	X	
Noturus insignis				2		1	4	15			3	X	X	X		
Lepomis auritus						2	4	5			1		X	X	X	
Lepomis gibbosus				1		5	8						X	X	X	
Lepomis macrochirus								4					X	X	X	
Micropterus dolomieui						1	2	3	1	1			X	X	X	X
Etheostoma olmstedi		2	14	36	3	3	23	2	1				X	X		
TOTAL SPECIMENS	23	135	384	370	122	148	257	210	116	22	31					

TABLE 2. Structural Redundancy Values Used in Calculating Inertia Indices for Each Stream Section of Conowingo Creek (e.g., 7 of 15 cyprinid fish species occured in Section I).

Families	Sections			
	I	II	III	IV
Cyprinidae (15)	7/15	9/15	15/15	8/15
Catostomidae (2)	2/2	2/2	2/2	1/2
Ictaluridae (3)	0/3	1/3	2/3	2/3
Centrarchidae (4)	0/4	1/4	4/4	2/4
Structural Redundancy	0.367	0.546	0.917	0.550

TABLE 3. Functional Redundancy Values Used for Calculating Inertia Indices for Each Stream Section of Conowingo Creek (e.g., 7 of 18 fish species which interacted at Trophic Level I occurred in Section I).

Trophic Levels	Sections			
	I	II	III	IV
I (18)	7/18	10/18	17/18	10/18
II (26)	10/26	14/26	25/26	13/26
III (22)	7/22	11/22	21/22	11/22
IV (10)	2/10	3/10	9/10	3/10
V (2)	1/2	1/2	2/2	1/2
Functional Redundancy	0.358	0.479	0.952	0.471

trophic level. For example, in Section I, there were 7 of 15 possible species from Trophic Level I; 10 of 26 at Level II; 7 of 22 at III; 2 of 10 at IV; and 1 of 2 at V. The mean functional redundancy for Section I was 0.358.

The mean structural redundancy value and mean functional redundancy value for each stream section were averaged. The value of Category B which was assigned to each stream section was based on this mean in the following manner: if the grand mean was between 0 and 0.2, a value of 1 was assigned; if it was between 0.2 and 0.4, a value of 1.5; between 0.4 and 0.6, a value of 2; if between 0.6 and 0.8, a value of 2.5; and if between 0.8 and 1.0, a value of 3 was given. Based on these data, Category B was assigned a value of 1.5 for Stream Section I, a value of 2 for Sections II and IV, and a value of 3 for Section III.

Stream order, flow dependability, and flushing capacity influence the value assigned to Category C. A value of 1 was assigned to Section I, because stream order and flow dependability generally increased as we moved downstream. The lowest reaches of the stream were characterized by extremely high gradient and, therefore, increased flushing capacity. Hence, a value of 2 was assigned to Section II, 2.5 to Section III, and 3 to Section IV.

The entire drainage basin of Conowingo Creek drains limestone rock, and the water is well buffered and antagonistic to toxic substances. Therefore, a value of 3 was assigned to all stations for Category D.

Category E was assigned a value of 2 for each station. Conowingo Creek is generally considered a "warm water" stream, although trout are stocked on a "put and take" basis by the Pennsylvania Fish Commission. Moreover, pH values were generally high. Thus a value of 2 was assigned since the system was not particularly close to a major ecological transitional threshold, at least with respect to its fishery.

To our knowledge, there is no basin management group which has established a monitoring program. Therefore, a value of 1 was assigned to Category F for each area.

Using the above information, an inertia index was calculated for each section as follows (Cairns and Dickson, 1977):

Stream Section	Inertia Index	= A x B x C x D x E x F
I	18	= 2 x 1.5 x 1 x 3 x 2 x 1
II	48	= 2 x 2 x 2 x 3 x 2 x 1
III	90	= 2 x 3 x 2.5 x 3 x 2 x 1
IV	72	= 2 x 2 x 3 x 3 x 2 x 1

The above example is a rough approximation of an inertia index. Moreover, it should be noted that the Conowingo Creek data were not collected for these types of analyses.

CALCULATIONS OF ELASTICITY INDICES

Cairns and Dickson (1977) define elasticity of a system as the capacity of a system to recover after a structural or functional displacement has occurred. The factors which they considered important in the development of an elasticity index are as follows: (A) existence of nearby epicenters for providing organisms to reinvade a damaged ecosystem; (B) mobility of any disseminules of the organisms present; (C) condition of habitat following the stress; (D) presence of residual toxicants; (E) chemical-physical environmental quality after pollutional stress; (F) management or organizational capabilities for immediate control of the damaged area.

Contrary to the calculation of the inertia indices, only three of the categories suggested by Cairns and Dickson (1975) can be used to calculate an elasticity index: A, B, and F. A stress must first occur before Categories C, D, and E can be used. Therefore, the index measures the potential of a particular section to recovery, where Elasticity Index = A x B x F. Again, each parameter was rated using a three-point scale.

Category A is a measure of nearby epicenters from which colonization can initiate should a stress occur. Section I was assigned a value of 2 for this category. If Section I were stressed, recolonization could take place from the lower stream reaches, where all the species which are present in this section also occur. A value of 3 was not assigned because recolonization could only take place in one direction (i.e., upstream). Using the same logic, a value of 3 was assigned for Section II. Recolonization could take place from two directions, upstream from Section III and downstream from Section I; and, all the species present in Section II also occur in either Section I or Section III. Section III has the richest fauna when compared to all of the other sections. Therefore, complete recolonization from the other section would not occur. Should the fauna in Section III be destroyed, complete natural recolonization would require migration of fishes from Conowingo Reservoir of the Susquehanna River. This would be a slow process since any fish must traverse the steep gradient of Section IV. A value of 1 was therefore assigned to Category A for this section. A value of 3 was assigned to Section IV; recolonization could come from either the Susquehanna River or from Section III, which has an extremely rich fauna.

A value of 2 was assigned to Category B for each stream section. Although fish are relatively mobile, they lack an aerial state (like most aquatic insects), therefore stream sections were not assigned a value of 3.

As stated earlier there are no management or organizational capabilities for immediate control of the area, with the possible exception of the Pennsylvania Fish Commission. Accordingly, a value of 1 was given for each section for Category F.

Through the use of these three categories, a crude elasticity index was calculated:

Stream Section	Elasticity Index	= A x B x F
I	4	= 2 x 2 x 1
II	6	= 3 x 2 x 1
III	2	= 1 x 2 x 1
IV	6	= 3 x 2 x 1

DISCUSSION

Cairns and Dickson (1975) suggest that a value of 400+ for the inertia index indicates high inertia; a value of 55-399, moderate inertia; and a value of less than 55 indicates poor inertia. A comparison of these ranges with the indices calculated for Conowingo Creek indicates that Stream Sections I and II have poor inertia, while Stream Sections III and IV have moderate inertia. Although these ranges are useful in comparing theoretical indices of broadly different ecosystems (i.e., ocean versus rivers), their usefulness diminishes when a practical application is undertaken. Therefore, any management decisions which evolve should be based on the relative values of the indices, rather than their location on an absolute scale.

A similar comparison of Conowingo Creek data could not be made for the elasticity indices since three of the parameters could not be used. It should be emphasized that the elasticity index is a measure of the potential of the system to recover, should a stress occur. The elasticity index is further limited by the paucity of information on dispersal rates of fishes. As information of this type becomes available, the use of this index will become more powerful; however, speed of locomotion is not necessarily correlated with ease of dispersal (Udvardy, 1969). Even with the inherent difficulties in the calculation of an elasticity index, a particular relationship between inertia and elasticity emerges. The area with the highest inertia index (Section III) had the lowest elasticity index. Although this relationship may not always exist (see Stauffer, *et al.*, in press), a management decision might evolve from this situation to stringently protect Section III so that it would be available to act as a refuge and, thus, an epicenter from which recolonization of other areas could initiate.

All of the parameters suggested by Cairns and Dickson (1977) can be used in the calculations of the inertia index. Additionally, since an inertia index can be calculated without the occurrence of a stress, it provides more information upon which to base management decisions. Therefore, the remainder of this paper will be limited to a discussion of inertia.

Category B (the structural and functional redundancy of the stream) is without a doubt, the single most important parameter upon which inertia is based. Since inertia is defined as the ability of a system to withstand a stress without eliciting a structural or functional change, it follows that the greater the redundancy in structure or function, the less chance a stress has of creating a measurable shift.

Functional redundancy was based only on trophic-level interaction. As more life history information becomes available for different fish species, other parameters can be included in the analysis, such as a characterization of the generalized habitat (i.e., pool versus riffle species; benthic versus surface inhabitants, etc.) Perhaps each life stage of the species present should be identified, counted, and analyzed separately. Because of the relatively few taxa present, structural redundancy was calculated by counting the number of species present in a particular family. If a more diverse fauna existed, or another major taxa used (e.g., aquatic insects or protozoans) it might be more applicable to count the number of species in a

particular genus. These indices must be calculated using different phyletic groups and applied to various ecosystems before a "best method" is determined.

Additionally, one might argue that both structural and functional redundancy are important enough to warrant separate categories. However, this raises the question of why structural redundancy values are included any place in the analysis. Although the intention of Cairns and Dickson (1977) is unclear, we have interpreted structural redundancy as being related to taxonomic groupings. If we assume a multidimensional niche concept as conceived by Hutchinson (1957), then it follows that taxonomic groupings are intimately related to niches. In fact, as indicated by the Gause principle, no two species can coexist for long if they occupy the same or very similar niches (Schoener, 1974). Schoener (1974), based on other studies (e.g., Hutchinson, 1959; Levins, 1968; Mac Arthur, 1965), makes the following generalizations: (a) since no two species can occupy the same niche, their niches are spaced along one or more important dimensions (e.g., food, habitat, etc.); (2) assuming an eventual incompressibility along any one dimension, there is an increase in the number of important dimensions with an increase in species number; and (3) a similarity of species along one dimension implies a dissimilarity along another. Since an organisms' niche is species specific and the niche is intimately tied to function, as indicated by the above generalizations, structural redundancy implies functional redundancy! Therefore, it would appear that the justification for including structural redundancy is based on the assumption that those taxa which are more closely related to one another, occupy more similar niches than those not closely related taxonomically. There are obvious exceptions due to convergent and divergent evolution. For example, a walleye and a tessellated darter, both of the family Percidae, occupy widely separated niches. These differences decrease if redundancy is calculated at the generic rather than at the family level. Darwin (1859; Diamond, 1978) realized this when he wrote:

> "As species of the same genus have usually, though by no means invariably, some similarity in habits and constitution, and always in structure, the struggle will generally be more severe between species, of the same genus, when they come into competition with each other, than between species of distinct genera."

On the other hand, when redundancy is calculated at the generic level, many genera which are represented by only a single species cannot be used, thus, information is lost. For example, in Conowingo Creek, there were three species (*Anguilla rostrata, Salmo trutta,* and *Etheostoma olmstedi*) which were not used in the calculation of structural redundancy. If structural redundancy were calculated at the generic level, information for twelve species would be lost.

Obviously, it would be ideal to study each organism in such a fashion that its niche could be described. If these niches could then be plotted in multidimensional space, overlap or redundancy could be precisely analyzed. However, practicality

requires that one rely on phyletic groupings and their relationship to functional redundancy if this classification scheme is to be used and applied. In fact, it may be that functional redundancy should be completely replaced by structural redundancy. Values for Category B would not change markedly if functional redundancy were ignored for the Conowingo Creek data.

As mentioned above, certain information is lost when calculating structural redundancy because a family or genus is represented by only one species. The possibility of including diversity indices into the calculation was considered because of this information loss.

Inertia and stability, by definition, are directly related. Although diversity indices have been related to community health (Patrick, 1949), their relationship to stability has not been experimentally demonstrated. However, as discussed by Emlen (1973), stable environments such as the ocean floor are characterized by high diversity (Sanders, 1968; Sanders and Hessler, 1969). However, this diversity may be explained by a geological time theory (Pianka, 1966; Emlen, 1973). Moreover, environmental stability led to high diversity; does high diversity in turn lead to increased stability? (For a more detailed discussion of stability theory, see Emlen, 1973). In any case, if the mean diversity indices (Table 1) for each stream section are included in the calculation of inertia, the values for each stream section are as follows: Section I = 18.1, Section II = 90.2, Section III = 210.8, and Section IV = 100. The respective order of each section was not changed relative to inertia. This is undoubtedly caused by the fact that those stream sections with the highest structural redundancy values also had the highest diversity. The effect of adding diversity indices to the calculations may be more dramatic in situations in which there is a greater number of higher taxonomic categories (i.e., more genera or families) represented by only a single species.

Another factor which might be considered for inclusion in the inertia calculations would be some measurement of productivity, either in the form of total numbers of organisms or a measure of biomass. If diversity indices are used, total number of organisms is considered to some extent, since diversity depends on community size; however, this factor is negligible in communities which have the same number of species with identical relative abundances (Pielou, 1977). A more exacting method for including a measure of the total number of individuals might be to employ an ordination technique as described by Hocutt (1975). This technique was used to graph each station (Figure 2). As indicated by Hocutt (1975), those stations in Quadrant III are the least healthy, while those in Quadrant II have the greatest health. Based on this, it might be feasible to enter a value of 1 for sections which fall in Quadrant III, a 2 for those in Quadrants I and IV, and a 3 for those in Quadrant II. Again, there is the problem of relating health to stability. Implementation of this procedure would reverse the inertia indices for Stream Sections II and IV.

CONCLUSIONS

The concept of inertia and elasticity as conceived by Cairns and Dickson (1975) can be used to formulate a stream classification system, which can predict the amount of stress a particular system can assimilate and the potential of a system to recover if and when the assimilative capacity is exceeded. In this particular example, we realize that a stress at any of the upstream stations would probably affect downstream areas; therefore, both inertia and elasticity indices would be more realistic if calculated for separate tributaries of a major drainage basin (see Stauffer, et al., in press). Before this system can be fully evaluated, these types of analyses must be applied to various ecosystems using different phyletic groups (e.g., phytoplankton, macroinvertebrates, etc.). Fish were used in this instance because data were available, but more importantly, because: (1) they occupy the top of the food chain in most stream systems, and, as such, their presence implies the presence of many other phyletic groups; (2) throughout their development from larvae through adult, they pass through most, if not all, trophic levels above the primary producer stage; (3) taxonomically, fish have been well studied, hence, accurate identifications can be made easily and quickly without the aid of sophisticated equipment; and (4) there is generally more information available on their life history than is available for other groups, so the relationship between structure and function is easier to compare than for other groups.

Finally, perhaps not all of the parameters used in the calculation of the indices should be multiplied. By varying the way and order in which parameters are treated (added or multiplied) different weights could be attributed to each parameter. Again more data must be analyzed before such a decision can be reached.

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