

## Unionids, fishes, and the species-area curve

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**Abstract.** The number of fish species in thirty-seven systems of the Ohio River may be predicted by the area of the drainage basin. On a large river system scale, the number of unionid species is directly related to the number of fish species present and, to a lesser extent, the drainage area. In small systems, such as headwater tributaries, the number of unionid species is related to the drainage basin area. Unionid diversity in systems intermediate in size may

be related to both. This may be the result of transient fishes in small streams depositing glochidia. The overall distribution and diversity of unionids within the study area is dependent upon the distribution and diversity of their fish hosts.

**Key words.** Zoogeography, Unionacea, Pisces, Ohio River, ecology, species-area curve, parasitology.

### INTRODUCTION

With very few exceptions, the unionid molluscs of North America require a fish host for their specialized larval stage, the glochidium. Metamorphosed unionids are essentially immotile and their limited movements as adults cannot be considered a method of dispersal. Alternative dispersal agents, such as transport on the feet of birds, are rare phenomena that have probably contributed little to the overall distribution of unionids (see review of Rees, 1965). It is the movement of fishes bearing glochidia that is the main mechanism of unionid dispersal, yet this is rarely addressed in the unionid distribution literature, with few exceptions (i.e. van der Schalie, 1945). For example, in an important paper on unionid zoogeography, Ortmann (1918) spoke of barriers to unionid dispersal, not barriers to fish dispersal. Members of unionid taxa are portrayed as having intrinsic distributions dictated by the same constraints as birds, insects, and other highly motile animals. This is not so. Unionids owe their distributional patterns to the superimposed ranges of their fish hosts.

The absence of mention of fish distribution in unionid research is largely the result of our ignorance concerning which fish (or fishes) is parasitized by each unionid species. Some, such as *Anodonta imbecillis* (Say, 1829) and *Strophitus undulatus undulatus* (Say, 1817) may metamorphose without a host (Lefevre & Curtis, 1911, 1912; Allen, 1924), but it is not known if this is their natural ontogeny or if successful parasitism in the laboratory reflects conditions in the field. Research in the area of host identification has become increasingly commonplace, but available data rarely allow for one-to-one comparisons of individual fish and unionid distributions.

There is a greater understanding of the systematics and zoogeography of North American fishes than there is for unionids. The level of zoogeographic synthesis found in Hocutt & Wiley (1986) for fishes has not been attained for

unionids, and published comprehensive faunal accounts for most North American taxa, such as Lee *et al.* (1980) for fishes, do not exist for unionids. The systematics of unionids in many areas, particularly the southeastern Coastal Plain and Gulf of Mexico drainages, are not well known.

The most comprehensive distributional data for both fishes (Mayden, 1988) and unionids exist for the central interior of North America, containing the Ohio River system, the subject of this paper. The recent availability of comprehensive unionid and fish distributional data from the central interior of North America allows a comparison of the two on a broad scale for the first time.

### METHODS AND MATERIALS

The diversities of unionids and fishes for forty-seven riverine systems were taken from literature sources listed in Table 1. The term 'unionid' is used throughout this paper, although the data include the single margaritiferid *Cumberlandia monodonta*. In this data set, thirty-seven systems are in the Ohio River drainage and ten are in the Maumee River system. Extinct and extirpated species are included where known and introduced fish species have also been included. Some fish data are based on counts obtained from maps given in the references and not from explicit estimates in print. Drainage areas are compiled from many sources not listed here, including hydrologic surveys and gazetteers. The data are cumulative in part, with each higher level including the area and species numbers of some, but not all, lower levels.

River systems were grouped in a hierarchical system. In this methodology, systems having a common confluence are grouped together with their parent stream despite size (Tables 2 and 3). Unlike using all systems of similar size from across the range of the data set, this method creates distributional units. All riverine systems considered here share a common master system and are

TABLE I. Drainage systems used in study.

System	Drainage area (km <sup>2</sup> )	Unionids		Fishes	
		No. of species	Source	No. of species	Source
Ohio River	530140	126	1,5,6	281	25
Allegheny River	30420	35	1	103	19
Cumberland River	47008	81	1	176	20,21
Eagle Creek (OH)	400	8	7	29	17
Green River	62156	71	1,32	147	20,21
Hocking River	3120	24	7	77	17
Kanawha River	31980	41	1,13,31	103	19,25
Elk River	3983	21	1,4,13,30	59	25
Pocatalico River	933	13	1,13	*	
Kinniconick Creek	658	17	8,32	72	21
Leading Creek	393	8	7	31	17
Licking River	9638	53	1,32	98	20,21
Little Miami River	4563	42	1	73	17
Little Scioto River	606	16	7	34	17
Muskingum River	20899	63	1,14,33	135	23
Ohio Brush Creek	1131	25	7	56	17
Pine Creek	481	11	7	29	17
Scioto River	16926	58	1	115	17
Big Darby Creek	1448	40	1,9,29	93	17,22
Hellbranch Run	94	6	9,29	36	17,22
Little Darby Creek	458	21	1,9,29	21	17,22
Proctor Run	29	4	9,29	17	17
Spring Creek	99	7	9,29	6	17
Treacle Creek	99	5	9,29	15	17
Robinson Run	31	4	9,29	*	
Sugar Run	10	5	9,29	10	17,22
Olentangy River	1397	31	1,10	74	17
Paint Creek	2969	24	11	69	17
Salt Creek	1438	29	7	81	17
Scioto Brush Creek	710	17	7	53	17
Shade River	575	8	7	46	17
Symmes Creek	926	18	7	59	17
Tennessee River	105560	96	1	224	20
Tygart Creek	884	31	12,32	56	21
Wabash River	31980	75	1,15,16,30	151	26
Embarras River	6331	39	27	48	24
Little Wabash River	8320	32	28	57	24
Maumee River	17123	38	2	*	
St. Joseph River	2756	35	2	56	17
Bear Creek (OH)	62	10	3	10	17
Eagle Creek	91	9	2,3	14	17
East Branch St. Joseph River	450	15	2,3	*	
Clear Fork	73	5	3	*	
Silver Creek	78	11	2,3	*	
Fish Creek	296	30	2,3	*	
Nettle Creek	140	7	3	*	
West Branch St. Joseph River	268	22	2,3	*	

Area of basin, includes lower level tributaries. Number of species recorded from system, includes lower level tributaries.

Source = literature source of number of species in drainage: 1, OSUM records (1990); 2, Watters (1988a); 3, Hoggarth (1987); 4, Ecological Specialists, Inc. (1991); 5, Williams & Schuster (1989); 6, Stansbery & Cooney (1985); 7, Watters (1988b); 8, Warren *et al.* (1984); 9, Watters (1986); 10, Hoggarth (1990); 11, Jennings (1969); 12, Taylor (1980); 13, Taylor (1983); 14, Stansbery *et al.* (1985); 15, Cummings *et al.* (1987); 16, Cummings, Mayer & Page (1988); 17, Trautman (1981); 18, Ecological Specialists, Inc. (1992); 19, Hocutt, Jenkins & Stauffer (1986); 20, Starnes & Etnier (1986); 21, Burr & Warren (1986); 22, Ohio Environmental Protection Agency records (1990); 23, Cavender & Ciola (1981); 24, Forbes & Richardson (1909); 25, Lee *et al.* (1980); 26, Burr & Page (1986); 27, Cummings, Suloway & Page (1988); 28, Cummings, Mayer & Page (1989); 29, Watters (1990); 30, Taylor & Hughart (1981); 31, Morris & Taylor (1978); 32, Cicerello, Warren & Schuster (1991); 33, Stansbery & King (1983).

\* - Data not available.

hydrologically and biologically connected. A species in any one level has at least the theoretical potential to disperse throughout that level. In this study, the Ohio River is broken down into decreasing levels as follows: Ohio

River > Scioto River > Big Darby Creek > Little Darby Creek. Note that the Ohio River level contains systems as small as Little Darby Creek, but unlike that system, they are immediately confluent with the Ohio River. Such a

TABLE 2. Hierarchical levels of river systems used in Fig. 7.

River level	Comparison	Slope of plot $z$	$r^2$	$P$	$N$
Ohio River	log(unionids)-log(area)	0.351	0.846	0.000	21
	log(fishes)-log(area)	0.291	0.906	0.000	21
	log(unionids)-log(fishes)	1.169	0.873	0.000	21
	unionids-fishes	0.458	0.922	0.000	21
Scioto River	log(unionids)-log(area)	0.297	0.616	0.065	6
	log(fishes)-log(area)	0.185	0.596	0.072	6
	log(unionids)-log(fishes)	1.558	0.970	0.000	6
	unionids-fishes	0.655	0.960	0.000	6
Big Darby Creek	log(unionids)-log(area)	0.465	0.873	0.020	5
	log(fishes)-log(area)	0.364	0.697	0.165	4
	log(unionids)-log(fishes)	0.747	0.502	0.292	4
	unionids-fishes	0.366	0.720	0.154	4
Little Darby Creek	log(unionids)-log(area)	0.614	0.892	0.056	4
	log(fishes)-log(area)	0.095	0.089	0.701	4
	log(unionids)-log(fishes)	0.776	0.145	0.620	4
	unionids-fishes	0.980	0.382	0.382	4

TABLE 3. Hierarchical levels of river systems used in Fig. 8.

River level	Comparison	Slope of plot $z$	$r^2$	$P$	$N$
Maumee River	log(unionids)-log(area)	0.045	NA	NA	2
St. Joseph River	log(unionids)-log(area)	0.388	0.690	0.021	7
East Branch	log(unionids)-log(area)	0.690	0.710	0.160	3

NA, not applicable, level has two points.

hierarchical system is necessary to evaluate distributional patterns. Levels chosen only by similar areas, without regard to dispersal patterns, from across the study area are mathematically coherent but may be biologically meaningless in this context. But because individual tributaries tend to occupy less area than their source river, the results may be very similar to levels chosen strictly by size.

River system hierarchies were constructed by taking a river and all systems *immediately* confluent with it, despite size, for which sufficient distributional data were available. Thus, the Tennessee River is contained in the same hierarchical level under the Ohio River, but Big Darby Creek is not. That river is in the level of the Scioto River. The data for a higher level contain information from the parent stream and the immediately lower level. Thus Big Darby Creek contains data for itself and its tributaries, including Little Darby Creek, but not individual tributaries of Little Darby Creek. Those streams are included in the level of Little Darby Creek. Because hierarchical levels contain subordinate levels, the data have a cumulative component in that points include data from other points. However, most levels also contain data unique to that level. The consequence of data of this type on regression analysis is not clear, but I believe the comparisons detailed in this study are valid.

Only two systems contained sufficient unionid distribution information at all levels to be used here: the

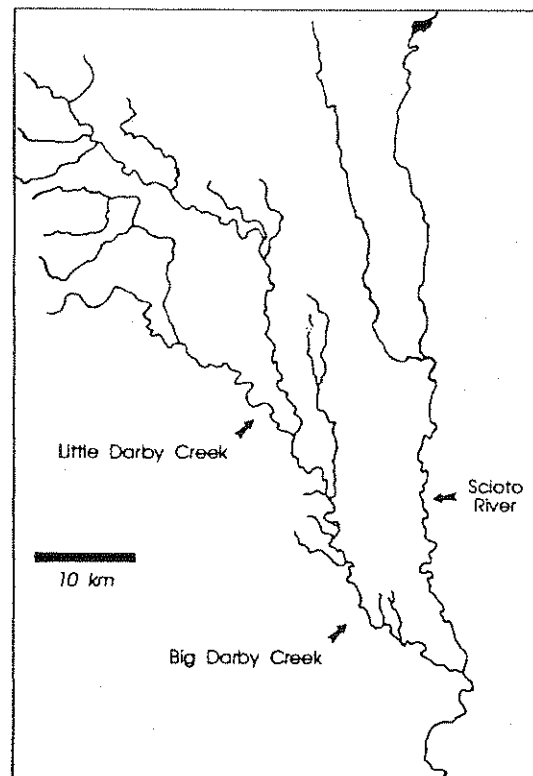


FIG. 1. The Big Darby Creek system

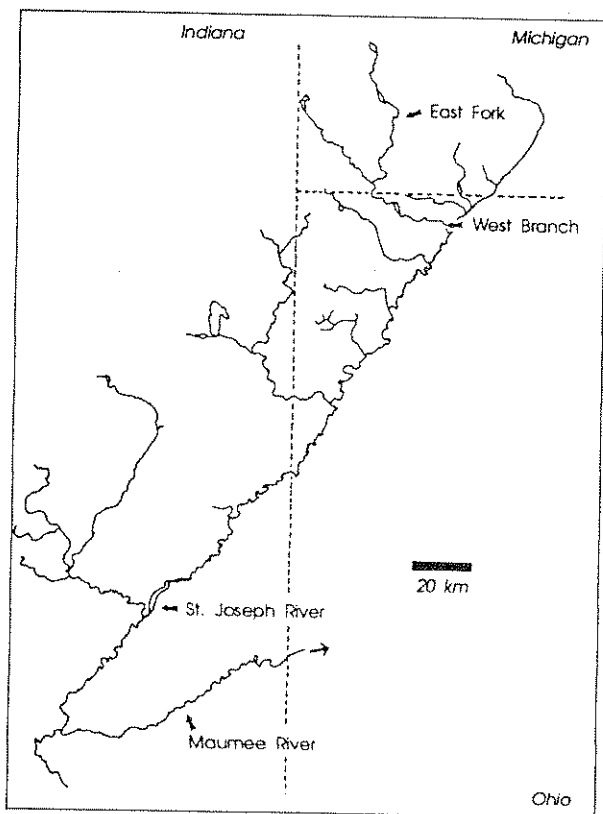


FIG. 2. The St Joseph River system

Little Darby Creek system of the Scioto River system in Ohio (Fig. 1) and the East Branch St Joseph River of the Maumee River in Ohio, Indiana, and Michigan (Fig. 2). The latter lacks fish distributional data for most levels.

The St Joseph River system of the Maumee River in Indiana, Michigan and Ohio recently has been surveyed for unionids (Watters, 1988b). Because the Maumee River was once a glacial outlet into the Wabash River, the unionid fauna bears more resemblance to the Ohio River fauna than it does to the Laurentian (Clark & Wilson, 1912; Walker, 1913) and has been included in this study of Ohio River species.

RESULTS

The plot of number of species of fishes on the species-area curve (Fig. 3) has the power function:

$$\text{No. of species of fishes} = (4.686 \text{ km}^2)^{0.322}; r^2 = 0.81; P < 0.0000.$$

This value of  $z$  (slope) falls within the range of 'Preston's canonical slope.' Preston (1962) had initially predicted a slope of 0.262, but additional studies have expanded its range of values to 0.15–0.40 (Williamson, 1988). This quantity may be thought of as the rate (on log-log plots) at which species 'fill' an available area. The slope increases with the number of species that occur in a given area.

Unionids show a similar species-area curve relationship (Fig. 3):

$$\text{No. of species of unionids} = (1.738 \text{ km}^2)^{0.343}; r^2 = 0.84; P < 0.0000.$$

The lines are essentially parallel (probability of  $b_1 = b_2$  is  $> 0.3$ ; t-test).

The species numbers of unionids and fishes are highly correlated on a linear plot (Fig. 4):

$$\text{No. of species of unionids} = 0.046 + 0.445 \text{ no. of species fishes}; r^2 = 0.92; P < 0.0000.$$

Correlations were analysed for each hierarchical level in the Ohio and Maumee River systems (Tables 2 and 3). Analysis of the partial correlations between numbers of fish species and unionid species and drainage area for these

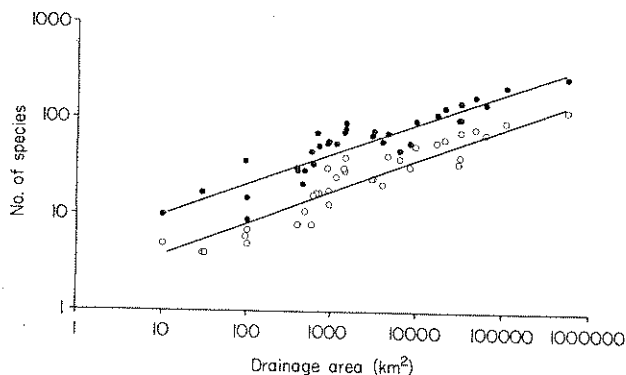


FIG. 3. Log-log plot of numbers of species of unionids and fishes. System drainage areas. ○, unionids; ●, fishes. Lines represent best fit power functions for each regression.

TABLE 4. Partial correlations coefficients (PC) of regression between Ohio River system fish and unionid diversity, and drainage area.

River level	Comparison	PC	Probability for N-3	N
Ohio River	unionid–fish	0.899	1%	20
	unionid–area	-0.161	>5%	20
Scioto River	unionid–fish	0.95	1%	13
	unionid–area	0.222	>5%	13
Big Darby Creek	unionid–fish	-0.363	>5%	7
	unionid–area	0.882	1%	7
Little Darby Creek	unionid–fish	0.315	>5%	4
	unionid–area	0.941	>5%	4

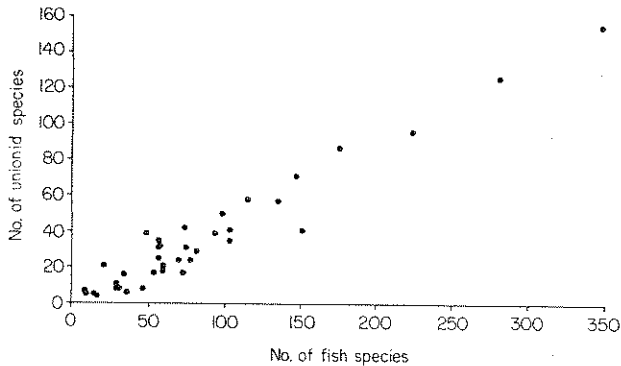


FIG. 4. Plot of numbers of species of fishes v. numbers of species of unionids for each drainage system.

levels suggests that most of the correlation is between fishes and unionids at large river sizes, while at smaller sizes unionid diversity is more correlated with drainage area (Table 4).

## DISCUSSION

### Fishes, unionids and drainage area

The relationship between the number of species in a given area and the size of the area was discussed by authors such as Jaccard (1908), Arrhenius (1921) and Gleason (1922). They found that larger areas contained predictably greater numbers of species. Since then this relationship, called the species-area curve, has been used with many scenarios, from marine fouling systems (Schoener & Schoener, 1981) to forest bird assemblages (Martin, 1988). Ecological explanations on the subject vary greatly. It is no longer solely regarded as an outcome of island biogeographic theory, a view once widely held, but is now thought to be a consequence of habitat heterogeneity. A few authors have criticized the relationship as a mathematical coincidence, notably Gilbert (1980, p.231) who remarked that there was 'little evidence to support its application to any situation.' Despite Gilbert's opinion to the contrary, research into the species-area curve relationship has continued, although along more rigidly defined methodological paths. Connor & McCoy (1979) have shown that experimental bias and mathematical coincidence did occur in some species-area curve studies and their criticisms have provided guidelines for subsequent species-area curve studies (see Wright, 1981).

The relationship between an area and the number of species contained in it has spurred an interest in environmental variables as additional or alternative predictors of species diversity. Some variables are better predictors than area in some instances. Angermeier & Schlosser (1989), in a study of freshwater fishes, found water volume to be a better predictor than drainage area, and numbers of individuals a better predictor than volume. Other workers have combined environmental variables with area in multiple regression analyses, with often apparently contradictory results. Angermeier & Schlosser (1989) found that habitat complexity variables did not increase appreciably the accu-

racy of species number predictions. Brönmark *et al.* (1984) reached a similar conclusion for non-unionid aquatic macroinvertebrates. Dillon & Benfield (1982, p.179), working with freshwater snails, stated that 'neither alkalinity nor water chemistry variables correlated with it directly limit the distribution and abundance of pulmonates [in their study area].' But, Brönmark (1985), also using aquatic snails, found that the inclusion of habitat complexity increased species number predictability. Swift *et al.* (1986) found a combination of area and density to be a better predictor than either variable alone for freshwater fishes. Rigby & Lawton (1981) and Boecklen (1986) also found habitat heterogeneity to be a good predictor of species number.

Only the drainage area variable was used in this study. The volume of water in each system has not been calculated and other environmental parameters have not been quantified for such a large study area. Fish diversity may be expected to be more related to drainage volume than to area in some studies (i.e. Angermeier & Schlosser, 1989). Fishes occur in the water column (a cubic dimension), and are not confined to the surface area of the drainage (a square dimension). This distinction may be significant in lakes and ponds, but usually the difference in volume is negligible in comparison to the total area, most systems being shallow relative to their areal extent. The use of drainage area for fishes is thus an acceptable approximation when dealing with large or multiple systems. Unionids, on the other hand, are confined to the substrate, the physical manifestation of the square dimensions of the drainage area. Thus, numbers of unionid species would be expected to correlate with drainage area more than with water volume.

Unionids show a species-area curve relationship similar to that of fishes. These lines are essentially parallel (Fig. 3). However, unionid diversity is not a consequence of drainage area. The high degree of association between unionids and area is at least partially the result of the correlations between fishes and drainage area, and between unionids and fishes. If numbers of fish species and drainage area are related, then unionid species are necessarily related if unionid and fish species diversity are correlated. This hypothesis can be tested using partial correlations between numbers of fish taxa, unionid taxa, and drainage area. Table 4 shows that for higher levels, most of the correlation lies between numbers of fish species and unionid species. The relationship between numbers of unionid species and drainage area is more important in smaller, lower level systems. Reasons for why this should be so are given in the next section. Strayer (1983) also found that unionid species richness was correlated with drainage area in Michigan. However, he concluded that 'stream size alone is obviously not sufficient to define the habitats of the two species' (p.258). That study did not look at fish diversity.

Further evidence that it is largely the relationship with fishes, and not drainage area, that determines unionid diversity may be found by examining rivers outside the Ohio River system. If unionid diversity is the result of drainage area, then rivers of similar area should have similar numbers of species, unrelated to the number of fish species. But if both numbers of unionid and fish species are differ-

ent from expected, and different in the same way, then there is circumstantial evidence that unionid diversity is related to fish diversity.

Three Texas rivers were plotted with the regression lines for the Ohio River system in Fig. 5: Trinity River/Galveston Bay, Brazos River, and Nueches River. Fish distributional data are from Conner & Suttkus (1986), unionid data are from Ohio State University Museum of Zoology records. The ichthyological fauna of Texas is not as diverse as that of the Ohio River system for a given drainage area. This may be due in part to improper habitats. But the unionid fauna also is less diverse, and depauperate in a graphically similar way to the fishes. Because it is unlikely that what constitutes an improper microhabitat for fishes also would apply to unionids, so it is improbable that unionid diversity would respond to drainage areas in the same manner as does fish diversity. If unionid diversity is not dependent upon fish diversity, then the numbers of unionid species might lie upon the unionid/drainage area line and not change with fish diversity. These preliminary results suggest that each river system or related region may have a different fish/unionid ratio.

It is the relationship between fishes and unionids that mostly determines the number of unionid species in river systems. The species numbers are highly correlated on a linear plot (Fig. 4). In this instance, the linear model explained more variation than did either the exponential or power function models. The ratio of fish species to unionid species based upon this equation differs from that derived by a comparison of species number ratio v. drainage area (Fig. 6). When diversities of both fishes and unionids are calculated from drainage area, the ratio of fish species/unionid species decreases from approximately 2.6 for a 10 km<sup>2</sup> area to about 2.1 for a 100,000 km<sup>2</sup> area. But when the relationship of unionid species is calculated from fish diversity, the relationship of the ratio to drainage area slightly increases. The ratio of numbers of species of fishes to unionids increases with increasing drainage system size, from approximately 2.22 for a 10 km<sup>2</sup> area to 2.246 for the 100,000 km<sup>2</sup> drainage area. By the latter method, the ratio of numbers of species of fishes/unionids is never less than 2.22, and apparently never more than 2.25, for all systems

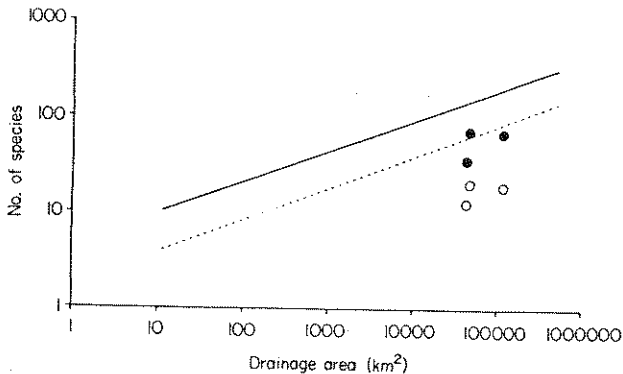


FIG. 5. Plot of regression lines for Ohio River system fish diversity (—), Ohio River system unionid diversity (---), Texas systems fish diversity (●), Texas systems unionid diversity (○), and drainage area (see text for details).

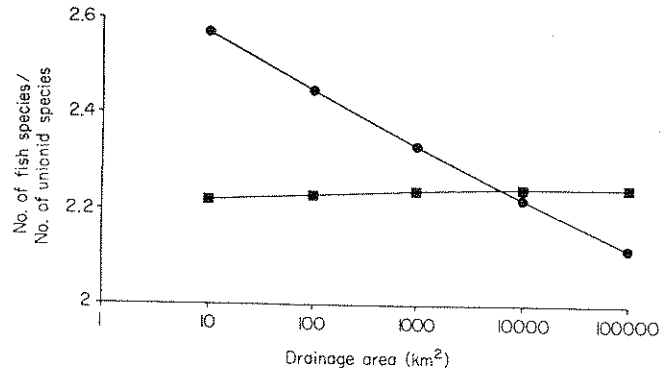


FIG. 6. Semilog plot of ratio of numbers of species of fishes/unionids v. system drainage areas. (●) Ratio based on relation between drainage areas v. both number of fish species and number of unionid species; (■) ratio based on relation between numbers of fish species v. numbers of unionid species

discussed in this paper. By either method, the ratio of fish species/unionid species ranges only between 2.6 and 2.1.

It is surprising that unionid diversity tracks fish diversity as closely as it does across such a wide range of system sizes. The species-area curve may be more complex than a single mathematical model can explain, yet departures from the species-area curve by fishes are reflected in unionid distributions and diversity. But how correlated are individual systems and subsets of the data set? Do unionid system diversities depart from those of fishes at any point?

### River system hierarchies

It is possible to partition the species-area curve for fishes into smaller subunits based upon a hierarchical design of confluent systems. In a hierarchic scheme from the Ohio River to the tributaries of Little Darby Creek, each level is a straight line segment of an overall curved line (Fig. 7; in actuality, each line also may be curved). The straight lines of Fig. 3 are artefacts produced as the result of curved lines superimposed on each other, and the procedure of calculating the best straight line through a curved one. For Little Darby Creek, the areas of the most headwater tributaries do not predict fish diversity accurately. The line is

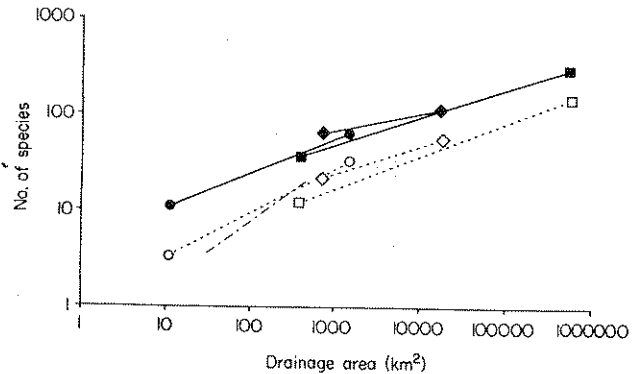


FIG. 7. Log-log plot of numbers of species of unionids and fishes v. system drainage areas based on system hierarchies for Ohio River system (see text for details). (—) Fish diversity; (---) unionid diversity. (●) Big Darby Creek; (◆) Scioto River; (■) Ohio River; (□) Unionids, Little Darby Creek

not significant and is not shown in Fig. 7. Each higher river system level has a lower slope, that is, the rate of species addition in the master or source systems is lower than the rate for the most removed systems tributaries. But because of the few degrees of freedom imposed by the low number of systems having data, the slopes of these lines are not different significantly. However, the fact that the fish and unionid lines approximate each other in a systematic fashion suggests that the phenomenon may be real. Future studies using greater numbers of systems statistically might bear out this result. In addition, a similar pattern has been noted in studies dealing with size area differences, such as those of Lassen (1975) and Haynes (1990), who found that smaller bodies of water have higher slopes than do larger ones for freshwater snails in their study areas. Higher slopes may be attributed to low immigration, a discontinuous increase in extirpation, low habitat diversity (Lassen, 1975) and predation (Martin, 1988). Although these factors may be responsible for the patterns seen for fishes in Fig. 7, only reduced immigration is physically related to dispersal. But because of the inherent correlation between drainage area and levels of confluence, strictly area-dependent factors such as habitat diversity cannot be excluded.

As before, the lines for unionids apparently parallel those of the fishes in each level, with two exceptions. First, while the line for fishes is not significant at the level of the smallest tributaries, the line for unionids is correlated with the area of these small drainages. This line continues the apparent trend of higher slopes seen in progressively lower levels. Second, the lines for unionids and fishes are not strictly parallel. At all levels for which there is sufficient data, the unionid line has a slightly higher slope than that of the fishes. However, these results are not statistically significant, and more data are needed to substantiate them.

The unionid lines for the hierarchical levels for East Branch St Joseph River show a similar pattern (Fig. 8), although the slopes are different than those of Little Darby Creek (Table 3). Each major drainage may have its own signature curve, and this possibility should be the subject of further study. Data for fish diversity are not complete for these drainages.

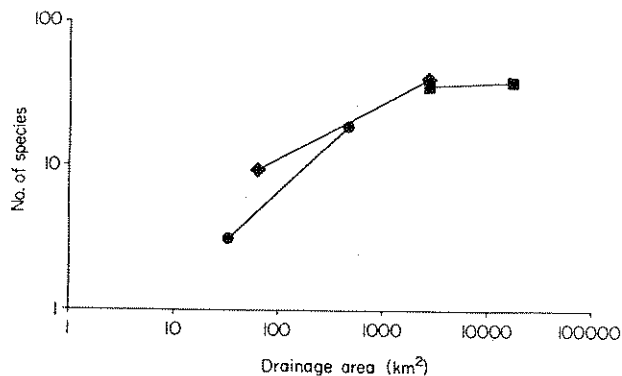


FIG. 8. Log-log plot of numbers of species of unionids v. system drainage areas based on system hierarchies for Maumee River system (see text for details). (●) East Branch St. Joseph River; (◆) St Joseph River; (■) Maumee River.

Dony (1977) and Connor & McCoy (1979) have pointed out that no one mathematical model may explain some species-area curves. Of the single models for linear, exponential, and power functions, the power function comes closest to the actual fish data in this study. However, large systems have fewer fish species than predicted by the species-area curve. Other factors apparently come into play at these drainage sizes that limit the total diversity, among them the apparent decreasing rate of habitat diversity in very large rivers.

The shape of the lines for unionids also suggests the curve detailed by Coleman (1981), and called the 'Coleman Curve' by Williamson (1988). In this model, the steep slope at small areas is the artefact, at least in part, of passive sampling. The model specifies that the species be randomly distributed within a sample and that the data be an actual representation of the sample's diversity, that is, the species must be completely enumerated. However, the data presented here do not fulfil the requirements of this model, although they may do so more than many studies of this kind. The first condition is not met in fishes or unionid data. The second may be fulfilled more in unionid studies, although realistically some species escape detection, particularly in larger rivers.

Differences between fish and unionid diversities may be attributable to several causes. Although unionids are essentially immotile, fishes are highly motile. Sampling of unionids reveals a more accurate assessment of the diversity of a particular site because unionids do not seasonally migrate, spawn in select areas, or abandon modified reaches. Sampling of fishes includes these transient individuals. At any one place and time, a fish sample may estimate inaccurately the number of species 'indigenous' to that area. This is especially true as one moves from major rivers into small headwater tributaries, and may be reflected in the higher fishes/unionids ratio in progressively smaller systems. If we consider some fishes to be transient in any given area, then those fishes may not be available for parasitization by glochidia by virtue of their absence during unionid spawning periods. This subset of fishes, unavailable to unionids, would increase the ratio of fishes/unionids at any level, but would be more important in progressively smaller systems that contain fewer total fish species. Alternatively, these fishes may deposit glochidia originating from other areas.

The presence of exotic and introduced fishes also may create a small discrepancy between the unionid-fish lines. Several unionids have been experimentally shown to infest the common carp and the guppy, and the margaritifera *Margaritifera margaritifera falcata* (Gould, 1850) now occurs in Lake Tahoe, Nevada, several hundred miles outside its natural range, as the result of the introduction of its host, a salmonid (D.H. Stansbery, 1990, pers. comm.). These instances must be considered the exception rather than the rule for there is no evidence that most unionids use exotic fishes as their major hosts. Courtenay *et al.* (1986) list forty-two established exotic fishes in North America, most beyond the study area of this paper. At any level, the presence of these species may represent another source of fishes unavailable to unionids. Still, the numbers of exotics

would contribute proportionately less in larger systems than in smaller ones.

The idea that some unionid species may metamorphose without a fish host is controversial. Although these species are widespread throughout different system levels, they are most common in extreme headwaters, where their 'direct' metamorphosis may be most beneficial. This would result in a lowering of the slope of the unionid lines at the lowest drainage areas, which would have the result of bringing the lines for unionids and fishes closer to parallel. This is not the case. These unionids may be facultative parasites that typically use a fish host, or as some authors have suggested, not be capable of metamorphosis without a host. In any event, the sampling biases of fish collections previously discussed may overshadow this reproductive strategy.

The differences in preservability of fishes and unionids also may be an important factor. Because unaltered unionid shells may exist for hundreds of years after the death of the animal, it is possible to detect unionid species that are extirpated from the river, or even extinct. This is usually not the case for fishes. Thus, the data may be biased against fishes for diversity estimates.

Finally, the headwater systems are the most unstable. They are more susceptible to droughts, floods, and fluctuations in water temperature, oxygen content, and pollution than are large rivers. At any one time, the fish and unionid faunas may represent only a short lived standing diversity. The lack of a correlation between fishes species and unionid species in headwater streams thus may be due to many causes.

## SUMMARY

The species-area curve relationship between fish and drainage area in the Ohio River system may be shown for systems for which there is sufficient distributional information. The curve may be divided into sections of river hierarchic levels based upon confluence patterns. Such arrangements should approximate distributional patterns in confluent streams. Each hierarchic level may be interpreted as a nearly straight line segment of the overall curve, with lower levels having greater slopes. The lowest levels of the fish species-area curve were not statistically significant in this study. This may be due to the transient nature of fishes in extreme headwaters and the sampling error associated with this phenomenon.

Most, if not all, unionids require a fish host for metamorphosis. Because of this, and because they are essentially immotile after metamorphosis, it is expected that the distribution of unionids should approximate those of their hosts. Although the number of available fish that are used as hosts is not known, the correlation between fish and unionid species is high at all but the lowest levels. In headwaters, the number of unionid species is more related to drainage area than to number of fish species. This is thought to be an artefact of fish sampling bias. The number of unionids in headwater tributaries is hypothesized to be related to the diversity of transient fish taxa there. Thus, the initial distribution of unionid species on *all* hierarchic levels is the direct result of their host fish distribution. Initial distribution here

refers to the placement of metamorphosed unionids by their hosts. The fate of the unionids after settlement represents a second 'layer' of dispersal dependent on immediate environmental conditions. Such a secondary distribution is the result of chance events such as droughts, impoundment, pollutants, and other agents. The distribution of unionids is primarily the consequence of host fish dispersal and secondarily the result of differential survival.

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