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ASPECTS OF CORBICULID-UNIONID SYMPATRY IN THE UNITED STATES

Arthur H. Clarke

ABSTRACT

The problem of elucidating some of the long term community relationships between introduced Corbicula fluminea and indigenous unionid populations in the United States is addressed in this paper.

We first examine the pertinent literature which, unfortunately, is comprised chiefly of accounts of unionid assemblages (with only incidental consideration of Corbicula) which are based principally on unitemporal or short-term observations in the Ohio-Mississippi and Atlantic Coastal Drainages. We also provide detailed data from unpublished studies on the Kanawha, St. Francis, James, Tar, and Neuse River Systems and discussions of those data.

Several major conclusions are reached. (1) The data indicate that after initial introduction in most natural water bodies in both the Ohio-Mississippi and the Atlantic Coastal Drainages, proliferation and rapid development of dense populations of Corbicula is to be expected, followed approximately 8 -12 years later by a distinct decline in densities. (2) In several Atlantic Coastal Drainage systems, widespread extinction of some unionid species has coincided in time and space with the development of dense Corbicula populations. (3) In most of the Ohio-Mississippi Drainage systems molluscan studies were carried out after Corbicula had peaked and had subsequently declined. These studies revealed that native unionid communities there still contained many species in substantial numbers. (4) Some Atlantic Coastal Drainage systems are sufficiently restricted in size that their endemic unionid species will probably become extinct because of direct or indirect competition with Corbicula. All refugia there might become dominated by Corbicula before that species exhibits significant population declines. (5)

The ecosystem approach for gaining insight into *Corbicula*- unionid interactions is more realistic than alternative methods and is likely to produce more useful results. (6) Students are urged to begin long-term studies of the few river systems which have not yet, but are likely to be invaded by *Corbicula*. Such systems offer important research opportunities for elucidating *Corbicula*- unionid interactions and other community changes. These opportunities are already limited and are rapidly disappearing.

INTRODUCTION

There are two questions relative to the spread of *Corbicula fluminea* (Mueller) in North America which have been vigorously debated by freshwater malacologists (*e.g.* Fuller, 1977; Rodgers *et al.*, 1977; Kraemer,1979; Counts,1983; Imlay, 1983; Clarke, 1986(a), 1986(b); Ahlstedt,1987; Bogan,1987; Neves, 1987). These are (1) is *Corbicula* likely to proliferate explosively after introduction into a previously unoccupied water body which is otherwise undisturbed and ecologically healthy and (2) once introduced, will *Corbicula* exert any significant impact on indigenous freshwater mussel populations. These questions are not only important ecologically, but they also have significant practical and legal implications for resource management and for the preservation of endangered species. Investigations directed toward answering these questions may also lead to new insights into the dynamics of interspecific interactions in freshwater communities.

During the past 30 years, and especially since 1980, it has been our privilege to carry out detailed mussel surveys in many river systems into which *Corbicula* has now penetrated. Some of those systems were studied while a *Corbicula* invasion was in progress and others were studied before and after, or only after, a colonization had occurred. The results of some of these studies are relevant to the *Corbicla*-unionid problem. They are reported here both for the purpose of contributing data for the present study and also as molluscan community status reports for those periods in time which they represent.

In this paper we shall review some of the voluminous literature on freshwater mussel populations and relate it to concurrent observations on Corbicula or to dates of invasion derived from other sources, report other pertinent observations based on our own experience, search for ecological and geographical correlations with the phenomena observed, and propose unifying principles for reconciling incongruities.

ACKNOWLEDGMENTS.- I thank my wife Judith for her invaluable assistance during all of the field work reported here. I am also grateful to Jane E. Deisler and Richard J. Neves for reviewing previous drafts of this paper, to John M. Bates for some original observations, and to the sponsoring agencies, the U.S. Army Corps of Engineers, the U.S. Fish & Wildlife Service, the Nature Conservancy and ESE, Inc. for their support. Other assistance is acknowledged in the agency reports cited herein. Some of the material included here was presented in lecture form during the 1987 and 1988 annual meetings of the American Malacological Union.

OBSERVED EFFECTS OF CORBICULID-UNIONID SYMPATRY

McMahon (1982), Counts (1983), and Neck (1987) have described and documented the spread of the introduced Asiatic clam Corbicula fluminea (Mueller) in the United States. In brief, C. fluminea was first found alive in North America in 1938, in the lower Columbia River in Washington. It appeared in California in the 1940's and 1950's, in the Ohio-Mississippi and Gulf of Mexico drainages in the 1960's and 1970's, and in the Atlantic Drainage in the 1970's and 1980's. We never found it in Canada during extensive field work throughout that country from 1959 to 1976 nor have other workers, not even in the Columbia River System nor in southern Ontario. (It has recently been found in and near hydroelectric plants in western Lake Erie (Clarke, 1981a) and in the St. Croix River along the United States shore (French & Schloesser, 1987), however, and it will probably soon occur in similar nearby habitats in southern Ontario). Perhaps more puzzling, however, is its limited spread in Mexico. Bequaert and Miller (1973) record it from western Mexico in Baja California and Sonora but only at a few sites very close to the U.S. border. Reports of *Corbicula* occurring in the Rio Grande River (known in Mexico as the Rio Bravo) were made as early as 1964, but in eastern Mexico *Corbicula* now extends southward for only about 200 miles, *i.e.* into the San Fernando and Soto la Marina drainages in Tamaulipas, We have not found it in the next drainage system to the south, the large Panuco River System, although we have searched there at many sites since 1985.

Numerous researchers have reported on the compositions of local unionid communities in the United States following invasion of those areas by *Corbicula*. Workers who have studied Pacific Coastal drainages (e.g. Fitch, 1953; Hanna, 1966; Hazel & Kelly, 1966; Eng, 1975; and Counts, 1983) have reported that huge, dense populations (some $>1x10^4/m^2$), although unstable, develop in many canals and drainage ditches there. No workers have reported on corbiculid- unionid interactions in that region, but unionid populations have long been rare in the southern portion of the Pacific Coastal Drainage and that is the region where *Corbicula* has been most intensively studied.

Reports of *Corbicula*- unionid communities in the Ohio-Mississippi System and parts of the Gulf of Mexico Drainage have been published by many authors but the majority of these have included little quantitative information. Several of the rivers studied had undergone obvious habitat degradation from pollution, cold water (hypolimnetic) discharge from vents located near the bases of dams, or from other causes. Although in some cases *Corbicula* was found to be abundant and unionids rare it is uncertain what role *Corbicula* played, if any, in the rarefaction of the unionids. Some of the rivers thus affected are the following: the Cumberland and Green rivers in Kentucky (impoundments and hypolimnetic discharges; Clarke, 1983a); Holston, Nolichucky, and Buffalo Rivers in Tennessee (pollution; Ahlstedt, 1986); Little Red River, Arkansas (impoundment) and Little River, Oklahoma and Arkansas (flooding and hypolimnetic discharge; both Clarke, 1987). In other rivers mussel die-offs have been reported but their causes are unknown; e.g., the upper Mississippi River (Thiel, 1987, Havlik, 1987), Powell River in Virginia and Tennessee (Dennis, 1985; Ahlstedt & Jenkinson, 1987), lower Tennessee River, Tennessee (Jenkinson, 1987), impoundments of the Niosho River, Oklahoma (Zale & Suttles, 1987) and in a number of other water bodies (Neves, 1987).

In many parts of the Ohio-Mississippi River System and in at least a portion of the Gulf of Mexico Drainage it is clear that species-rich mussel communities occur together with *Corbicula fluminea.* without any apparent negative effects on the former caused by the latter. Ahlstedt (1986) has described several such instances in the Tennessee River Drainage based on exhaustive field studies by him and other scientific staff of the Tennessee Valley Authority. The most notable of these was observed in the Clinch River in Virginia and Tennessee where 141 survey sites studied from 1978 to 1983 yielded a total of 43 species of Unionidae. *Corbicula* also occurred there and was reported as "widespread and common". Two tributaries of the Clinch, the Powell River and Copper Creek, were also studied in 1979 and 1980 and yielded 37 unionid species (78 sites studied) and 19 species (36 sites), respectively. At the time they were surveyed *Corbicula* was observed to be "rare" in them. (It should be noted, however, that in 1983 and 1986 mussel die -offs occurred in the Powell River; the mussels were emaciated and had an unknown brown substance on their gills (Ahlstedt & Jenkinson, 1987)). Other Tennessee River tributaries studied by TVA in 1979 and 1980, all of which contained *Corbicula* (relative abundance not reported), were the Elk River in Tennessee and Alabama (38 unionid species, 108 sites studied); Duck River, Tennessee (35 species, 99 sites); and Paint Rock River, Alabama (35 species, 28 sites).

Many other workers have described similar associations in the Ohio-Mississippi drainage. Miller, Payne, and Siemsen (1986) reported 26 species of unionids living in the Ohio River at Olmstead, Illinois, along with *Corbicula*. Quantitative samples (24 0.25m^2 quadrats) yielded mean densities of 66 unionids/m^2 and 1475 *Corbicula*/m^2. Taylor (1980) reported 18 species of unionids living with *Corbicula* in Tygart Creek (an Ohio River tributary in northeastern Kentucky) and Taylor & Hughart (1981) also reported 18 species of unionids co-occurring with *Corbicula* (characterized as "common") in the Elk River in West Virginia (most sites were in Clay County), a tributary of the Kanawha River which flows into the Ohio River. (In 1978 we searched the Elk River at 2 sites in Clay County and found *Corbicula* to be rare (<1/m^2)). DiStefano (1984) reported 22 species of unionids living with *Corbicula* in Horse Lick Creek (a tributary of the Rockcastle River, which flows into the Cumberland River) and Starnes & Bogan (1982) reported 24 species of unionids, and *Corbicula*, living in Little South Fork Cumberland River (another Cumberland River tributary). Starnes & Bogan's work also included a quantitative sampling program: transects at 3 different sites (10 triplicated samples in each transect) revealed unionid densities of 7.5, 7.2, and 2.9 per m^2 and corresponding *Corbicula* densities of 46.6, 43.7, and 10.8 per m^2. Miller & Harris (1987) reported 24 species of unionids, and *Corbicula*, living in the White River near Newport in Jackson and White Counties, Arkansas. Mussel densities ranged from 4 to 44 specimens per m^2 and *Corbicula* were "rare". (In 1984 we searched the 2-mile reach of the White River just above Aberdeen, Monroe County, Arkansas. A dense unionid bed occurred just opposite Aberdeen but unionids were rare elsewhere and no *Corbicula* were seen.) Cooper (1984) studied 4 oxbow lakes of the Mississippi River in Arkansas and found 15 unionid species and a species of *Musculium* living with

Corbicula in one lake, 5 species of unionids plus *Corbicula* in another, 4 species of unionids in a third but without *Corbicula*, and 3 species of unionids in a fourth which also lacked *Corbicula*. Hartfield & Rummel (1985) recorded 36 nominal species of Unionidae, and *Corbicula*, from Big Black River, a Mississippi River tributary in Mississippi. See also papers by Branson & Batch (1969) and Clench & Stansbery (1963), discussed below.

Pertinent recent studies on Gulf of Mexico drainage systems are rare. Miller, Payne, & Aldridge (1986) reported that a mussel bed in the Tangipahoa River had 5 species of unionids (density 1.24/m^2) plus *Corbicula* (8.93/m^2). According to Fuller (1977), based on extensive field work, W. H. Heard has concluded that *Corbicula* may have been responsible for the reduction and/or extinction of certain mussel species in the eastern part of this region. See also the paper on the Alabama River by Hubricht (1966) discussed below, for comments on *Corbicula*.

Some malacologists working in river systems in the Atlantic Coastal Drainage have reported a different phenomenon from that frequently seen in the Ohio-Mississippi Drainage. Their observations indicate that, at least in some apparently healthy river systems, soon after *Corbicula* first invades a river it quickly develops very extensive and dense populations (e.g. $>1x10^3/m^2$) and that in such situations native unionids appear to be drastically affected. Gardner *et al*. (1976), in a detailed quantitative study (discussed below) reported that in the Altamaha River, Georgia, *Corbicula* achieved densities of 10^3 to 10^4 per m^2 about 4 years after it was first introduced there and that a concurrent decrease in unionid and sphaeriid populations also occurred (from a maximum of about $10^2/m^2$ decreasing to zero). Fuller (1977), writing on the endangered and threatened mollusks of North Carolina, warned that *Corbicula* will probably become a serious menace to the native unionids. Clarke & Neves (1984) in a report to the U.S. Fish & Wildlife Service, provided evidence that the proliferation of *Corbicula* in the James River System in Virginia coincided with a drastic decline in the native unionid fauna and he proposed a cause and effect relationship. Further general information about the apparent serious effects of Corbicula on mussels in the James, Tar, and Neuse Rivers were published soon thereafter (Clarke, 1986a, 1986b) but quantitative data were not included.

DETAILED CASE STUDIES

KANAWHA RIVER, WEST VIRGINIA

In September, 1982 ECOSEARCH, Inc. carried out a mussel survey (Clarke, 1982) of the upper part of the Kanawha River in Fayette County from the Falls of the Kanawha near Glen Ferris (RM 95.5) to the railroad bridge near Falls View (RM 90.9). See Figure 1, From June 28 to July 1, 1987 we performed another survey there, in an area a little downstream from the railroad bridge (RM 90.5 to 90.2) at the village of Montgomery Heights. On both occasions the work was carried out principally by SCUBA divers under our supervision, but crowfoot dredging, toeing, shallow water searching with a viewing box, and examination of muskrat middens was also done where appropriate.

The reaches surveyed were not ecologically uniform and it is useful to consider that part of the river as comprised of 6 smaller reaches. These are: (1) the turbulent plunge pool and adjacent ponded area just below the falls (RM 95.5-95.1); (2) the rather deep and strongly flowing reach extending from Reach 1 to the rapids (RM 95.1-94.5); (3) the rapids (94.5-93.0); (4) another fairly deep, strongly flowing reach extending from the rapids to the mouth of a tributary, Paddy Branch (RM 93.0-92.0); (5) a similar reach extending from Paddy Branch to the railroad bridge (RM 92.0-91.0); and (6) the reach below the railroad bridge at Montgomery Heights (RM 90.5-90.2). (We have not surveyed the reach between RM 91.0 and 90.5). The water depths and bottom sediments in those reaches

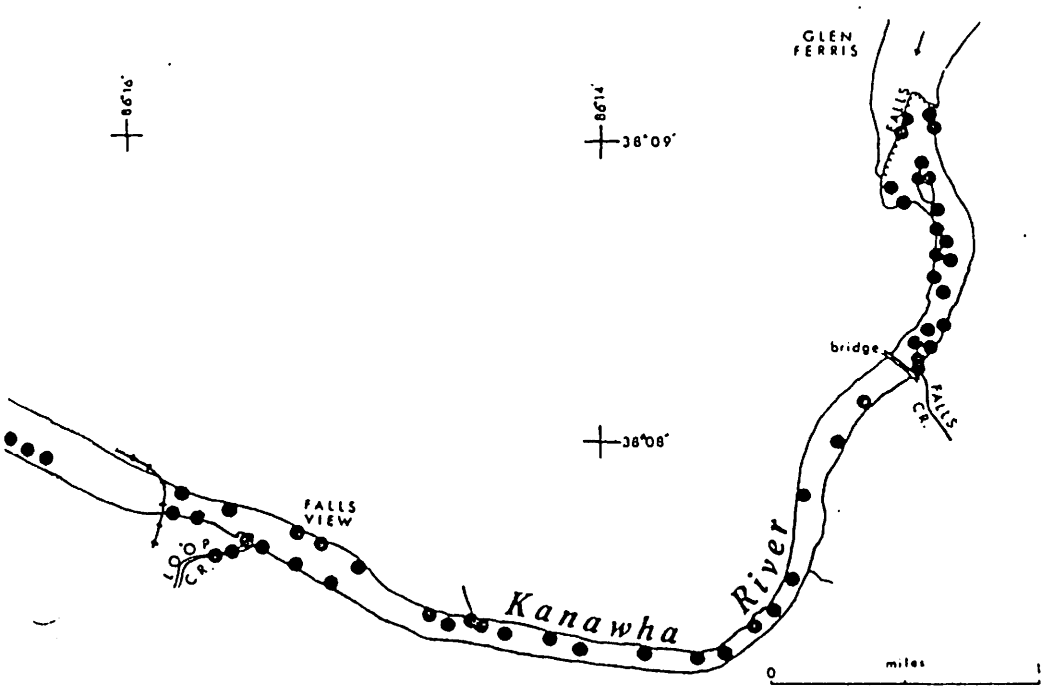

Figure 1. Study sites in the Kanawha River, Fayette County, West Virginia. Center of area shown is about 25 mi SE of Charleston, West Virginia.

TABLE 1
SPECIES COMPOSITIONS, EXPRESSED IN PERCENTAGES, OF UNIONID FAUNAS IN 6 REACHES OF THE KANAWHA RIVER, WEST VIRGINIA

REACH NO.	1	2	3	4	5	6	(N)
LIVE SPECIMENS (N)	(28)	(633)	(70)	(101)	(113)	(567)	
Amblema plicata	0	32	24	11	2	45	(488)
Actinonaias carinata	7	24	14	31	9	10	(256)
Fusconaia subrotunda	0	6	4	3	25	14	(154)
Obovaria subrotunda	14	10	+	0	3	0.7	(77)
Quadrula pustulosa	11	8	3	0	11	2	(76)
Ptychobr. fasciolare	0	1	10	16	15	5	(75)
Lasmigona costata	18	4	11	23	0	1	(66)
Elliptio dilatata	21	2	11	2	20	2	(66)
Elliptio crassidens	0	0.3	6	1	1	7	(46)
Potamilis alata	0	0.8	3	0	0	6	(43)
Ligumia recta	0	5	+	2	2	0.4	(35)
Lampsilis ovata	18	2	+	9	1	+	(28)
Leptodea fragilis	4	3	+	0	0	0.5	(26)
Cyclon. tuberculata	0	0.3	+	2	5	2	(21)
Tritogonia verrucosa	0	0	3	0	0	3	(19)
Lampsilis fasciola	4	0.3	9	1	5	0.2	(16)
Anodonta grandis	0	0	0	0	0	0.7	(4)
Strophitus undulatus	0	0.3	0	0	0	0.4	(4)
Lampsilis abrupta	0	0.5	0	0	0	0	(3)
Pleurobema cordatum	0	0.2	0	0	1	0	(2)
Plethobasus cyphyus	0	0.2	0	0	0	0.2	(2)
Megalonaias gigantea	0	0.2	0	0	0	0	(1)
Obliquaria reflexa	4	0	0	0	0	0	(1)
Cyprogenia irrorata	0	0	1	0	0	0	(1)
Truncilla truncata	0	0	0	0	0	+	1 shell
Totals	101	100.1	99	101	100	100.1	(1510)

were: (1) to 5 m deep, boulders, gravel, and sand; (2) to 6 m, cobbles and gravel; (3) to 1 1/2 m, boulders with gravel and sand in interstices; (4) to 5 m, cobbles and gravel; (5) to 5 m, also cobbles and gravel; and (6) to 4 m, gravel. All of the mussels found during systematic surveys were tabulated (Table 1) and these results therefore accurately reflect relative species abundances. A few additional species, found during non- quantitative reconnaissance work, are indicated by a + in Table 1.

Corbicula fluminea was first observed in the Kanawha River (at Charleston, W.Va.) in 1961 (Thomas & Mackenthum, 1964). During our 1982 and 1987 surveys its maximum density appeared to be about 10 to 25/m^2. Corbicula shells were very abundant in muskrat middens in 1982, along with hundreds of unionid shells of at least 11 species. In 1987, however, middens were composed almost entirely of thousands of Corbicula shells. The only unionid shells there were 4 valves of Obovaria subrotunda and 2 valves from smooth juvenile specimens of Quadrula pustulosa, all of which somewhat resemble large Corbicula.

ST. FRANCIS RIVER, ARKANSAS.

In the fall of 1984 and the summer and fall of 1985 ECOSEARCH, Inc. carried out a mussel survey of a 53-mile portion of the lower part of the St. Francis Floodway(1) in Cross, St. Francis, and Lee Counties (Figure 2). Our work was done principally while low water conditions prevailed and most of the bottom

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(1) An explanation of terms is necessary. A half-century ago, for reasons of flood control, the meandering St. Francis River was divided into 2 major waterways by a long levee, in the same manner that a dollar sign is produced by a stroke through an S. The severed ends of the meanders west of the levee were joined by canals thereby forming the "St. Francis Floodway". The meanders east of the levee were similarly linked by canals and that configuration retained the name "St. Francis River".

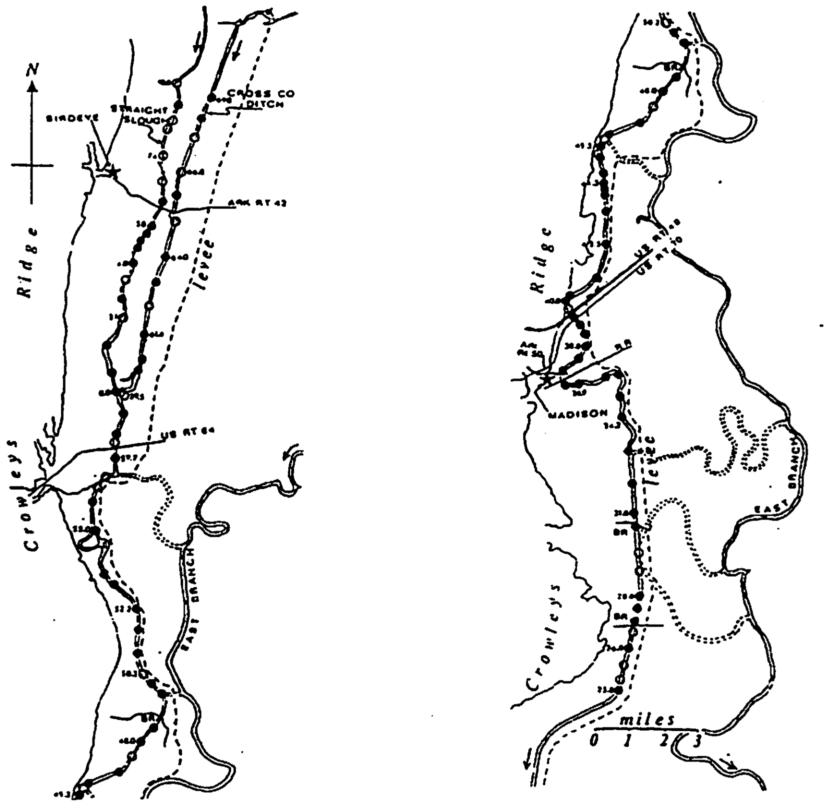

Figure 2. Study sites in the St. Francis (River) Floodway, Arkansas. Left figure is northern portion of area and right figure is southern portion. Numerals represent river-mile designations. Area shown is about 40 mi W of Memphis, Tennessee.

TABLE 2

RELATIVE COMPOSITIONS, EXPRESSED IN PERCENTAGES, OF UNIONID FAUNAS IN 6 REACHES OF THE ST. FRANCIS FLOODWAY, ARKANSAS

REACH NO.	1	2	3	4	5	6	(N)
LIVE SPECIMENS (N)	(83)	(67)	(138)	(13)	(813)	(62)	
Amblema plicata	0	0	30	0	36.9	0	{342)
Potamilis capax	47	42	20	31	13.9	18	(222)
Potamilis laevissimus	12	15	17	54	11.2	15	(151)
uadrula pustulosa	1	0	1	0	12.3	14	(111)
Potamilis purpuratus	2	9	6	8	6.4	24	(89)
Leptodea fragilis	12	25	12	0	3.0	11	(75)
Lampsilis anodontoides	0	3	2	8	4.7	5	(47)
Quadrula quadrula	2	1.5	1	0	2.7	0	(27)
Megalonaias gigantea	0	0	7	0	2.1	0	(26)
Lampsilis ventricosa	0	0	2	0	1.6	0	(16)
Tritogonia verrucosa	0	3	1	0	1.1	3	(14)
Pleurobema cordatum	0	0	0	0	1.4	0	(11)
Quadrula nodulata	4	0	0	0	0.9	0	(10)
Anodonta grandis	10	0	0	0	0.2	0	(10)
Obliquaria reflexa	0	0	1	0	0.2	8	(8)
Fusconaia flava	0	0	0	0	0.7	0	(6)
Pleurobema coccineum	0	0	0	0	0,4	0	(3)
Lasmigona complanata	4	0	0	0	0	0	(3)
Fusconaia ebena	0	0	0	0	0.1	0	(1)
Quadrula metanevra	0	0	0	0	0.1	0	(1)
Leptodea leptodon (?)	0	0	0	0	0	2	(1)
Lampsilis fasciola	0	0	0	0	0.1	0	(1)
Truncilla truncata	0	1.5	0	0	0	0	(1)
Totals	100	100	100	101	100.0	100	(1176)

could be reached without diving. A viewing box, mask and snorkel, toeing, and other tactile methods were used and all mollusks within a series of measured areas (ordinarily 1000m²) were collected, tabulated, and returned to the river. This portion of the St. Francis Floodway can be usefully considered as comprised of 6 distinct reaches, each of which is chiefly characterized by whether it lies within a part of the old river channel or within a recently-built canal. The reaches are: (1) a tributary channel (mostly comprised of a canal) formed by Straight Slough and the upper part of St. Francis Bay north of Cross County Ditch, from its mouth to a point 10 mi upstream, in Cross County; (2) a large canal, Cross County Ditch and the lower part of St. Francis Bay, all part of the main floodway channel in Cross County (RM 69 to 57); (3) part of the old river channel in Cross County (RM 57 to 49); (4) another large canal, Clark Corner Cutoff, in Cross and St. Francis Counties (RM 49 to 46); (5) another segment of old river channel, in St. Francis County (RM 46 to 33); and (6) another broad canal, the Madison-Marianna Diversion, in St. Francis and Lee Counties (RM 33 to 25.8).

The approximate river width, water depth, current speed at time surveyed, and bottom sediments in these reaches were: (1) 50 m wide, to 2 m deep, current slow, bottom sand and mud; (2) 75-100 m, mostly >2 m, moderate to slow, mostly sand; (3) 50-80 m, to 2.5 m, slow, sand and mud; (4) 50-60 m, 1.5 m, slow, mud and clay; (5) 50-60 m, 2 m, slow, mud and sand; (6) 100 m, >2 m, moderate, mud and some sand. Approximate total areas searched in each reach were: (1) 16,500 m², (2) 19,400 m², (3) 12,400 m², (4) 2,030 m², (5) 13,800 m², and (6) 5,100 m².

The relative compositions by species of faunas in individual reaches, the total numbers of mussels found in each reach, and other totals are given in Table 2. The mean numbers of living unionids found per 1000 m² area in each reach were (1) 5.0, (2) 3.5, (3) 11.1, (4) 6.4, (5) 58.9, and (6) 12.2. Reach 5, a portion of the river still within the old river channel, also contained by far the largest number of species (20) and also harbored mussel beds of substantial size and density. The reaches within parts of the old river channel supported an average of 36.2 living mussels per 1000 m^2 of bottom surveyed, whereas those reaches occupying canals supported an average of only 6.8. For further details see our manuscript report (Clarke, 1985).

The earliest records for *Corbicula* in the St. Francis drainage were reported by Counts (1983) based on specimens in the Ohio State University Museum, viz. (a) St. Francis River at Marked Tree, Poinsette County, Arkansas, collected in 1966, and (b) St. Francis Floodway in the Madison-Marianna Diversion Channel, collected in 1974. These localities are (a) about 15 mi above our search area and (b) within our search area. Our 1984 and 1985 records of its occurrence in each reach are: (1) none, (2) 1 specimen, (3) 3, (4) none, (5) common at 1 site (RM 33.6) but only 6 seen elsewhere, and (6) 2.

JAMES RIVER SYSTEM, VIRGINIA AND WEST VIRGINIA

This large system was surveyed throughout most of its length in the region above Richmond, Virginia in 1984 (see Figure 3, also the unpublished report by Clarke and Neves, 1984). A local area near Richmond was also studied in 1987[2]. During the first survey the work was done with snorkels and face masks, with viewing boxes, and by tactile methods. Access to tributaries was from local roads, but since road access to the main channel of the James River was insufficient, most of its length above Richmond was

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(2) The localities searched near Richmond in 1987 are: (Station 2332), Tuckahoe Creek, 1/2 mi above mouth, Henrico and Goochland Counties; (Sta. 2333), James River near Lower Tuckahoe and Shooters Hill, about 1 mi SW of Lorraine, Henrico Co.; (Sta. 2334), James River, about 2.5 mi E of Watkins Landing, Goochland Co.; (Sta. 2335), Tuckahoe Creek, from railroad tracks to 1/4 mi upstream, 1.0-1.2 mi above mouth; and (Sta. 2335A), Tuckahoe Creek, 1.4 mi above its mouth, both Henrico and Goochland Counties.

floated by canoe. In 1987 a dive boat and 2 SCUBA divers were used in the main channel near Richmond and wet suits and viewing boxes were used in Tuckahoe Creek.

The study sites in the James River System group naturally into 3 categories: (1) upstream tributaries ((A) Potts Creek System, (B) Jackson River System, (C) Cow Pasture River System, (D) Johns Creek-Craig Creek System,and (E) North (or Maury) River System), (2) downstream tributaries ((A) Rivanna River System and (B) Tuckahoe Creek), and (3) the main channel of the James River ((A) the extensive reach above Sabot, Va. surveyed in 1984 and (B) the reach near Richmond, Va. studied in 1987). The general results of the sampling program are given in Table 3 under those headings. Substrata in upper tributaries and the Rivanna River were principally of cobbles, gravel, and sand; those in the James River of sand and mud nearshore and of gravel in depths exceeding 2 m, and in Tuckahoe Creek they were of sandy mud or mud. Additional ecological data are given in Clarke and Neves (1984).

According to Diaz (1974) Corbicula was first introduced into the James River System in 1971 in the James River near Hopewell, Prince George County, Virginia, about 15 mi below Richmond. By 1972 it had attained a population density exceeding 1000 individuals per square meter in the vicinity of Hopewell and had occupied the James River throughout a reach extending at least from Richmond downstream for 35 miles and a reach of the Appomattox River (a James River tributary) from its mouth to 8 miles upstream. In 1984 we found that Corbicula occurred throughout the James River from Richmond to the mouth of Craig Creek, a distance of about 180 miles, and to have attained population densities exceeding 1000 per square meter at many localities within this reach. In 1984 it also occurred in the Rivanna River from its mouth upstream at least 10 miles and in similar densities. It was entirely absent from Craig Creek and from the other tributaries farther upstream in the James System. By 1987 it had ascended about 2 miles up Craig Creek but was rare there. At that time it also

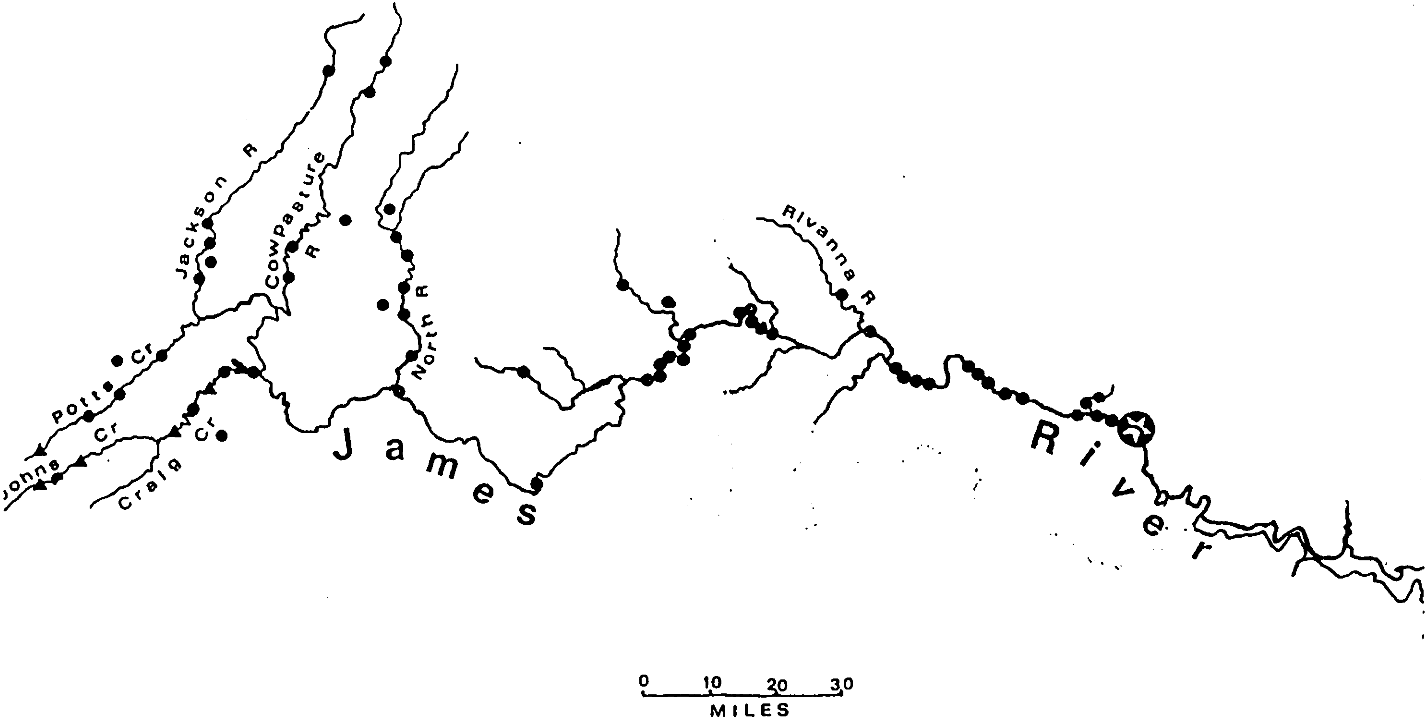

Figure 3. Study sites in the James River System, Virginia and West Virginia. The star symbol within a circle represents Richmond, Virginia.

TABLE 3

RELATIVE COMPOSITIONS, EXPRESSED IN PERCENTAGES, OF UNIONID FAUNAS IN 9 REACHES OF THE JAMES RIVER SYSTEM, VIRGINIA AND WEST VIRGINIA[3]

REACH NO.	1A	1B	1C	1D	1E	2A	2B	3A	3B	(N)
LIVE SPEC. (N)	(48)	(73)	(11)	(379)	(144)	(18)	(183)	(754)	(983)	
Ellip. complanata	0	0	0	5	0	100	62	99	100	1883
Villosa constricta	0	49	36	38	8	0	0	0	0	197
Stroph. undulatus	50	4	0	14	28	0	0	0	0	120
Anodonta cataracta	0	0	0	0	62	0	7	0	0	101
Canthyria collina	50	0	0	17	0	0	0	0	0	88
Ellip. lanceolata	9	47	64	7	2	0	7	1	0	87
Alas. undulata	0	0	0	16	0	0	0	+	0	62
Ellip. fisheriana	0	0	0	0	0	0	24	0	0	45
Fusconaia masoni	0	0	0	3	0	0	0	0	0	10
Totals	100	100	100	100	100	100	100	100	100	2593

(3) Corbicula densities in these reaches were : 1A, 1B, 1C, 1D, 1E, none; 2A, 3A, 3B, abundant; 2B, few.

occurred in Tuckahoe Creek from its mouth at least to a point 1.6 miles upstream but in low densities (about 10 to 50 per square meter). Tuckahoe Creek specimens were all blackened and apparently stunted.

TAR RIVER SYSTEM, NORTH CAROLINA

This interesting, medium-sized system was studied during numerous trips during the period from 1977 to 1983. Some aspects of the work have been described by Clarke (1983b), 1986(a), 1986(b), and Johnson & Clarke (1983). Access was achieved from local roads and bridges where possible, supplemented by several river runs surveyed by canoe. A total of 72 study areas were searched, some on several occasions (see Figure 4). Critical areas were sampled quantitatively by marking off 100 by 100 foot areas and tabulating all mollusks within them, or by means of transects, as appropriate. Collections were made with viewing boxes or by tactile methods and all data were recorded on standard data sheets.

The system studied may be considered as comprised of the following 7 ecologically distinct reaches: (1) the upper Tar River from its headwaters in Person County to the boundary between Franklin and Nash Counties, (2) the upper middle Tar River from Reach 1 to a little above the Rocky Mount Reservoir, all in Nash County, (3) a transition zone between the river and the reservoir containing species characteristic of both habitats, in Nash County, (4) Rocky Mount Reservoir, Nash County, (5) the lower middle Tar River, from the reservoir to just below Town Creek at North Carolina Route 42, 6 mi S of Tarboro, all in Edgecombe County, (6) the lower Tar River, from Reach 5 to tidewater, in Edgecombe and Pitt Counties, and (7) Fishing Creek, the largest tributary of the Tar, in Edgecombe County. The average widths, depths, and substrate types in these reaches were: (1) 5-10 m, <1 m, mostly gravel, some sand; (2) 10-20 m, 1.5 m, sand and gravel; (3) river backed up from reservoir, 10 m, 2 m deep, mud; (4) large reservoir,deep mud; (5) 30-60

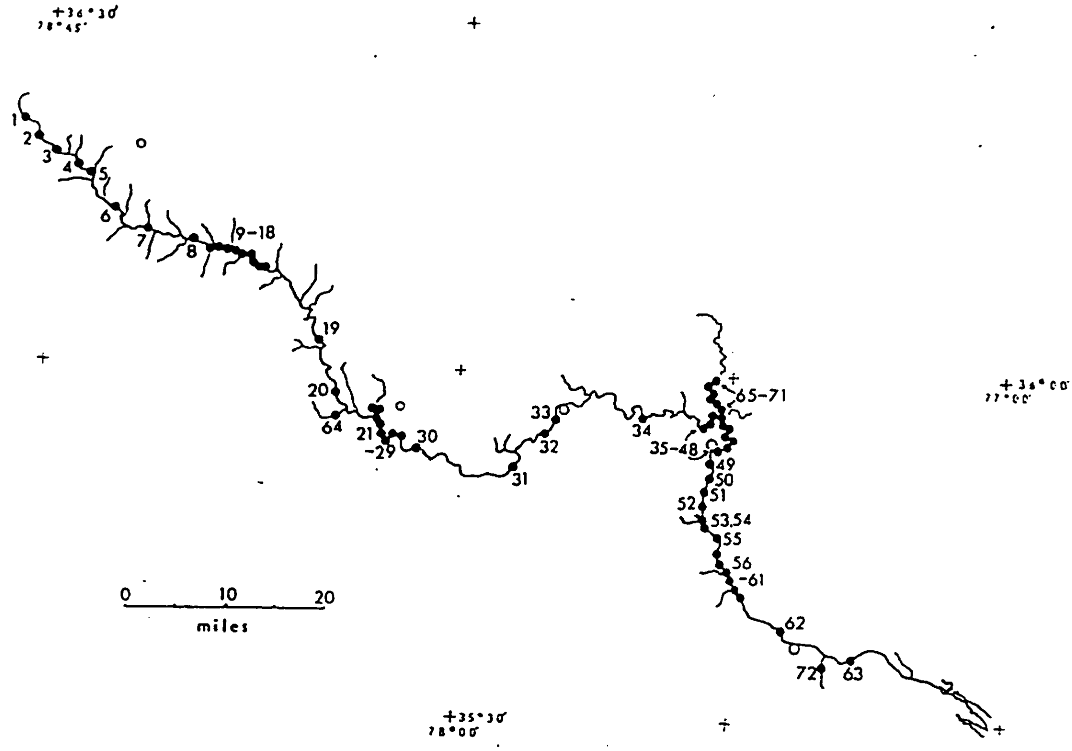

Figure 4. Study sites in the Tar River System, North Carolina. Small open circles represent cities, e.g. the circle near Station 5 indicates Oxford, Granville County and that near Station 48 indicates Tarboro, Edgecombe County.

m, 2 m, sand; (6) 50-75, 2-2.5 m, muddy sand and mud; (7) 5-25 m, 1-1.5 m, sand and muddy sand. Site numbers shown of Map 4 correspond to these reaches as follows: (1) contains sites 1 to 20, (2) contains 21-30, (3) contains Site 31, (4) contains 32 & 33, (5) contains 34-53, (6) contains 54-63, and (7) contains 65-71. (2 other sites, 64 and 72, were on small tributaries and were unproductive; they are omitted here).

The early phase of the spread of _Corbicula_ in this system occurred while our work was in progress. In 1977 and 1978 extensive searches throughout the whole river did not reveal any _Corbicula_, nor did our work in 1980 (which did not include Reach 6). In the summer of 1982 _Corbicula_ was found to be abundant (10^2-10^3/m^2) in the whole lower Tar River (Reach 6) and to have penetrated about 10 river miles upstream (density there about 10^2/m^2) to a point 2 1/2 mi below N.C. Route 44 (north of Tarboro). In the summer of 1983 a few specimens (density about 10/m^2) occurred in the Tar River about 50 miles farther upstream, near U.S. Route 64 near Spring Hope, Nash County. At that time they had also penetrated Fishing Creek to a point 5 miles above its mouth.

Neves (1987: 8-10) states the following: " A survey for the Tar River Spiny Mussel (_Canthyria steinstansana_) was conducted from April 28 to May 1, 1986, in Edgecombe, Nash, and Franklin Counties, North Carolina, by myself and biologists from several state and federal agencies. During this survey we found evidence of a recent die-off in the Tar River above Rocky Mount, Edgecombe County, that had affected all species and sizes of mussels in this river reach. So many shells of freshly dead mussels littered the river bottom, that I easily filled four 20 liter buckets with shells from a 100 m section of the river immediately upstream from the sewage treatment outfall at Rocky Mount. As judged by the presence of the adductor muscles on many of the shells, the die-off probably occurred in early to mid-April. A cursory evaluation of live versus dead mussels indicated that at least 50 to 75% of the mussels at this site had died. Snail and limpet populations appeared to be present in normal abundance, and the Asian Clam was

TABLE 4
RELATIVE COMPOSITIONS, EXPRESSED IN PERCENTAGES, OF UNIONID FAUNAS IN 7 REACHES OF THE TAR RIVER SYSTEM, NORTH CAROLINA

REACH NO.	1	2	3	4	5	6	7	(N)
LIVE SPECIMENS (N)	286	254	22	28	121	121	70	
Elliptio complanata	71.3	70.0	59.0	7.0	62.0	93.4	91.4	(649)
Lampsilis ochracea	5.3	1.2	9.0	0	27.3	4.1	1.4	(62)
Elliptio lanceolata	13.6	7.1	14.0	0	0	0	0	(60)
Anodonta imbecilis	0	0	18.0	93.0	0	0	0	(30)
Lasmigona subviridis	2.5	5.1	0	0	0	0	0	(20)
Fusconaia masoni	3.1	2.4	0	0	0.8	1.7	0	(18)
Lampsilis cariosa	0	6.7	0	0	0	0	1.4	(18)
Alasmidonta undulata	1.4	2.4	0	0	0	0.8	2.9	(13)
Canth. steinstansana	0	0	0	0	9.1	0	0	(11)
Villosa constricta	0	4.3	0	0	0	0	0	(11)
Strophitus undulatus	1.0	0.8	0	0	0.8	0	1.4	(7)
Alasmidonta heterodon	0.3	0	0	0	0	0	0	(1)
Anodont. ferussacianus	0.3	0	0	0	0	0	0	(1)
Lampsilis radiata	0	0	0	0	0	0	1.4	(1)
Totals	99.8	100	100	100	100	100	99.9	(902)

abundant and apparently unaffected."

NEUSE RIVER SYSTEM, NORTH CAROLINA

Field studies in this river system were carried out at 18 stations during the years 1977, 1983, and 1985, See Figure 5. Additional station data was also provided by Mr. Andrew G. Gerberich. Historical information has been published by Walter (1958) and Johnson (1970) and additional data about our work are available in Clarke (1986(b)). As in other systems, the study stations fall into a few natural groups, viz. Reach 1, the middle Neuse River in Wake and Johnston Counties (7 stations); Reach 2, the lower Neuse River in Wayne and Lenoir Counties (4 stations); Reach 3, Little River (4 stations); and Reach 4, Trent River (3 stations). Ecological data on width, depth, and substrate are: Reach 1, 10-20 m, 1.2-1.5 m, sand with mud at edges; Reach 2, 50-80 m, 1.5->2 m, sand & mud; Reach 3, 10-20 m, 0.5-2 m except at 1 site, a riffle, with depth 0.1-0.2 m, sand & mud except for the riffle where the bottom was of slabs and cobbles; Reach 4, 15-30 m, 1.0->2 m, mud (and pollution at 2 sites).

Access was from roads and bridges, gear consisted of a canoe, wet suits, and viewing boxes and collections were made principally by visual means supplemented at some sites by tactile methods. The Trent River was badly polluted by oil and trash and no mollusks were found in it. The Neuse River near Goldsboro, Wayne County, was similarly polluted but no pollution was observed elsewhere in the Neuse River or in the Little River.

Corbicula was widespread in the Neuse River but its date of introduction there is unknown. It was observed in 1983 to be common or abundant only at the 3 sites just above Goldsboro and the site just below it, and at the 2 lowermost sites in the Neuse, and this may indicate introduction within the previous 3 or 4 years. The observation that it was very rare near Seven Springs in Lenoir County in 1983, but abundant ($10^3/m^2$) there in 1985, supports that view. In the Little River *Corbicula* occurred (about $50-100/m^2$)

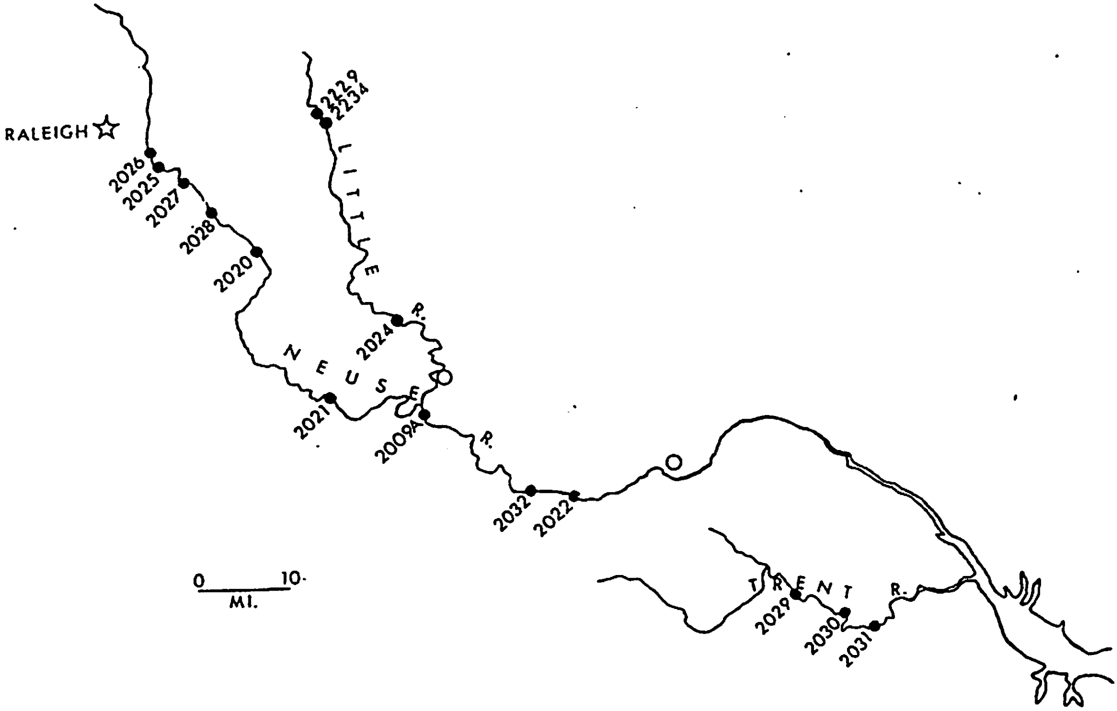

Figure 5. Study Sites in the Neuse and Trent River Systems, North Carolina. Small open circle near Station 2009A indicates Goldsboro, Wayne County and that E of Station 2022 indicates Kinston, Lenoir County.

TABLE 5

RELATIVE COMPOSITIONS, EXPRESSED IN PERCENTAGES, OF UNIONID FAUNAS IN 3 REACHES OF THE NEUSE RIVER SYSTEM, NORTH CAROLINA

REACH	Middle Neuse R.	Lower Neuse R.	Little R.	(N)
Live Specimens (N)	(55)	(57)	(107)	
Elliptio complanata	96	94	78	(190)
Ellip. cistelliformis	0	0	10	(11)
Elliptio lanceolata	0	0	7	(8)
Elliptio judithae	4	2	0	(3)
Alasmidonta undulata	0	0	3	(3)
Lasmigona subviridis	0	0	2	(2)
Fusconaia masoni	0	4	0	(2)
Totals	100	100	100	(219)

only at the lowermost site, at 2 mi N of Princeton in Johnston County, which also indicates recent introduction to the Neuse River System.

DISCUSSION

All available information indicates that the relative compositions of Corbicula-unionid communities in non-degraded reaches of the Ohio-Mississippi Drainage, although diverse, are generally quite different from those in non-degraded reaches in the Atlantic Coastal Drainage. (Insufficient data are available on Gulf Coast and Pacific Drainage bivalve communities to allow generalizations to be made). In the Ohio-Mississippi Drainage Corbicula is almost ubiquitous but its present populations there , with few exceptions, tend to be of only moderate densities and many species of unionids are often seen to occur with them. In the Atlantic Drainage Corbicula is not universally distributed and where it does now occur it is frequently seen in exceedingly dense concentrations. In those Corbicula-infested areas unionid populations are ordinarily absent or comprised principally of only 1 species.

We believe that partial explanations for these contrasts may be sought through elucidation of some aspects of population development in Corbicula and through consideration of the possible effects of Corbicula on community food webs.

TEMPORAL ASPECTS OF CORBICULA POPULATION CHANGES

The only quantitative, multiyear study of a bivalve community, during the period immediately following the introduction of Corbicula, is that of Gardner et al (1976) on the Altamaha River in Georgia. Corbicula first appeared in the upper Altamaha in 1971, and during the 4 year period beginning just before Corbicula was seen there, a quantitative sampling program was carried out. A series of quantitative samples were taken at 2 to 4 transect sites in the RM 113-118 reach at approximately 6-week intervals using a modified Petersen grab which samples a bottom area of 0.025 m^2. *Corbicula* population densities rose rapidly but irregularly and reached summer maxima of about 100/m^2 in 1972, 700/m^2 in 1973, 10,000/m^2 in 1974, and 400/m^2 in 1975. Populations of other bivalves, which consisted mostly of sphaeriids but also contained unionids, declined irregularly from maxima of about 22/m^2 in 1971 and 1972 to about 10/m^2 in the fall of 1973 and 0 by the summer of 1974. (In June,1988 we visited a locality on the Altamaha a few miles downstream from the RM 113-118 reach (at Morris' Landing, ca. 12 mi NE of Baxley, Appling Co., Ga.) during extreme low water conditions. A careful search of that wide, sandy area, lasting 1.5 hours, revealed *Corbicula* throughout most of the area in moderate numbers (ca. 25-50/m^2) but increasing to about 100-200/m^2 in muddy nearshore sites. Only 2 young unionids, in the mesoconch stage, were found and no sphaeriids were seen).

The only other changes in densities of *Corbicula* which have been studied quantitatively are periodic die-offs, phenomena which affect some, or perhaps eventually all, populations which develop densities greatly exceeding 1000/m^2. Some of these die-offs are believed to have been caused by unusually cold winter temperatures (Bickel, 1966; Sickel,1986) or by unknown physical or chemical factors. Others, however, probably resulted from maturation of high density juveniles which, as observed by Sickel (1986), produced constantly-moving, multilayered concentrations in which many individuals died, an event which led to oxygen depletion and mass mortality. One such event occurred in the Tennessee River in Kentucky in 1977 (Sickel & Heyn, 1980). The *Corbicula* population there consisted of abundant, very large (>60 mm) individuals but after the crash it was replaced by a dense population (1800/m^2) in which adults did not grow beyond about 12.3 mm. We believe that this may be another example of restricted growth (stunting) which has been observed in other freshwater mollusks living in habitats in which metabolites from previous populations, or densely-packed coexisting individuals, have accumulated (see Clarke, 1973 for references to previous work on this phenomenon). The stunting of Corbicula which we observed it Tuckahoe Creek (James River System) may also have resulted from this effect.

A survey of publications in which quantitative observations are reported for individual points in time reveals an interesting trend which apparently applies to bivalve communities in both the Ohio-Mississippi and the Atlantic Drainages. Nearly all cases in which Corbicula was reported as "paving the bottom", "exceedingly abundant", described in similar extreme terms, or at densities of more than $1000/m^2$, represent localities in which that species had been introduced within the previous 1 to 8 years (Bates, 1962; Branson & Batch, 1969; Clench & Stansbery, 1969; Cohen, *et al*, 1984; Diaz, 1974; Gardner, *et al*; 1976; Grace & Buchanan, 1981; Gunning & Suttkus, 1966; Hubricht, 1966; Schneider, 1967, and this paper (Tar River)). The period from 9 to 12 years after initial introduction was represented by only 1 record, *viz*. Catawba River, N.C. ($39-493/m^2$, McLeod & Sailstad, 1981). Nearly all of the reports which represent observations of populations more than 12 years old appear to indicate markedly reduced densities. In those reports Corbicula is described as "very common" ((Elk River, W.Va., Taylor & Hughart, 1981); "common" (Clinch River, Va. & Tenn., Ahlstedt, 1986); occurring in densities from about 10 to $50/m^2$ (Ouachita River, Ark.,Clarke, 1987; Tangipahoa River, Miss.,Miller *et al*, 1986; Little South Fork Cumberland River, Ky., Starnes & Bogan, 1982; and Kanawha River, W.Va., this paper); "rare" (Powell River, Va. and Copper Creek, Tenn., Ahlstedt, 1986); or occurring in densities of less than $10/m^2$ (White River, Ark., Miller & Harris, 1987; Middle Fork Little Red River, Ark. and St. Francis River, Ark., both this paper). The only exceptions are populations in the Powell River, Va. described as abundant about 20 years after introduction (R.J. Neves, pers. comm.); the Ohio River at Olmstead, Ill. cited as having a density of $1475/m^2$ 21 years after introduction (Miller, Paine, & Siemson, 1986) and Tennessee River, Ky.(Sickel, 1986, see above).

Available information, such as it is, therefore indicates that in the Atlantic, Gulf of Mexico, and Ohio-Mississippi River Drainages a similar pattern of rapid increasen in population density following introduction probably applies throughout. This is followed by a gradual decline (after about 8-12 years) at most localities and by massive die-offs in some, notably in very large rivers. In a few rivers about 20 years after introduction resurgences occur during which densities exceeding $1000/m^2$ may again be achieved. In some of these instances stunting may occur. Information about the nature and frequency of resurgences is insufficient to determine if it is a general phenomenon, however.

COMMUNITY FOOD WEBS

A stochastic diagram of a food web in a simple freshwater ecosystem is shown in Figure 6. The general pathways of energy flow are shown as broad arrows, the interspecific pathways by solid lines, and host-parasite relationships are shown as broken lines. Three species of unionids and their 3 fish host species are thus indicated. The first fish species feeds on mollusks, the second on zooplankton, and the third on benthic insects. Several kinds of phyto-plankton and other algae, representing several body size groups, are also included. They are fed upon by zooplankton, phytophagous insects, unionids, and sphaeriid clams. Postlarval unionids are also fed upon by carnivorous benthic insects(3). Other interactions

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(3) In most freshwater ecosystems, mature and immature benthic insects provide the greatest source of taxonomic and behavioral diversity and temporal variability. More than 100 insect species are typically found in any given ecosystem. Phytophagous chironomids ordinarily dominate but many carnivorous groups, such as Odonata, Megaloptera, many Coleoptera and Hemiptera, and some Diptera (e.g. tabanids and carnivorous chironomids) are also present. Most of the insect species exhibit very large cyclic density changes throughout the year (see,e.g., Hynes, 1970).I

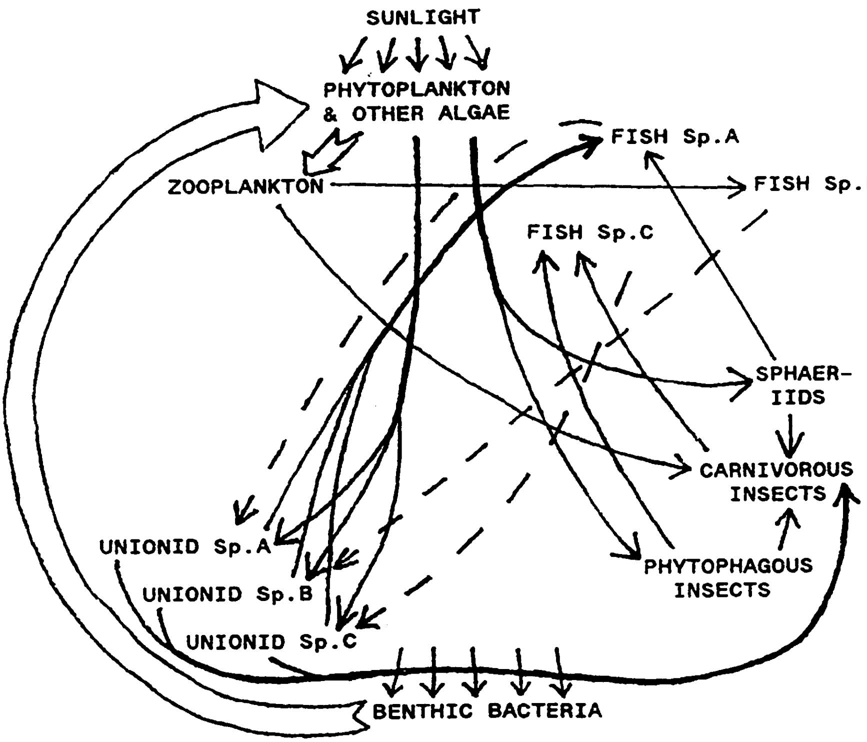

Figure 6. Simplified trophic diagram (food web) for a freshwater community prior to invasion by Corbicula. To avoid confusion the important roles of Protozoa and other zooplankton as food for unionids and sphaeriids, and the contributions of other organisms (macrophytes, crustaceans, etc.) to the trophic network, have been omitted. See text.

within the system, including nutrient recycling by bacteria, are also indicated. Although we have omitted mammals, amphibians, reptiles, birds, gastropods, benthic crustaceans, protozoans, other invertebrates, and macrophytes from the diagram, in real situations many of those groups are also important.

Although many scenarios are possible, let us assume that Corbicula are released into this ecosystem by a fisherman who cracks open an adult Corbicula and impales it on a hook. This action might release hundreds of larvae. Assuming that the water body is chemically and physically suitable for Corbicula, their survival would depend on the densities of micropredators at that point in time, especially carnivorous benthic insects and other arthropods. In general, ecosystems with high productivity are more likely to have large standing stocks of these predators than those of moderate or low productivity.

Let us consider a situation in which a few Corb-

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believe that the intensity and the quality of predator pressure which they may exert on juvenile mollusks will also show corresponding shifts.

It should be stated that it has not been demonstrated that benthic insects feed on mollusks. indirect evidence suggests that they probably do. Unionids and carnivorous aquatic insects have existed together at least since the early Tertiary It therefore seems overwhelmingly likely, given the great diversity of potential predators on the one hand, and the predictable presence every year of tiny juvenile unionids on the other, that predator- prey relationships have evolved. Further, the fact that various configurations of beak sculpturing occur throughout the Unionidae, but that consistent configurations occur only within species or genera, indicates that beak sculpturing features are adaptive and not recapitulations of ancestral history. Beak sculpture ridges clearly strengthen the shells of tiny juvenile unionids against crushing and would function as a defense against small shell-crushing predators of body sizes similar to those of many benthic insects.

icula have survived beyond the larval and juvenile stages. In a highly productive ecosystem with large native molluscan populations and a complex biotic community, long-term dominance by *Corbicula* might not be possible because dense populations of benthic insects and other invertebrates would feed on larval and young post-larval *Corbicula* and several species of molluscivorous fishes, and some mammals and birds, would feed on subadults and adults. The share of phytoplankton and other algae consumed by *Corbicula* would therefore be only moderate and sufficient food for indigenous unionids would still be available. *Corbicula* feeding might even compensate for the algae consumed by the enhanced efficiency in nutrient recycling which *Corbicula* might provide.

In contrast, let us consider what might happen in an ecosystem where productivity is moderate or low, indigenous mollusk populations are not large or dominant, and predator populations are not dense and do not depend heavily on mollusks for prey. Such ecosystems are natural and commonplace in the Atlantic Coastal Drainage and in some other areas. (Of course reduced productivity can also be produced by pollution, channelization, and other human activities). In such habitats predator pressure would be reduced, the great biotic potential of *Corbicula* would not be effectively constrained, and its population densities might soon become great and might remain so for several years. Feeding by such large concentrations of *Corbicula* would undoubtedly remove most of the algae of acceptable size groups from the water column. This would surely lead to a great reduction in the volume of algae available for other animals which depend on it directly, *i.e.* for zooplankton, many phytophagous insects, sphaeriids, and unionids, and to significant population declines in these animals. Secondary and tertiary effects would soon follow and populations of carnivorous insects and of fishes which feed on zooplankton and benthic insects must also decline. Such shifts would exacerbate the trend toward dominance by *Corbicula* by reducing predator pressure even further on its larvae and juveniles. This would cause a further reduction in other herbivores, which would further reduce populations of *Corbicula* predators, and so on and so on.

Such a scenario, of course, would also exacerbate the trend toward elimination of those unionids which use planktivorous and insectivorous fishes as their glochidial hosts. In fact, this phenomenon might be responsible for the dramatic decline in the unionid *Elliptio crassidens* (Lam.) in the Tennessee River which has been observed by J. Bates & S. Dennis (pers. comm.). That mussel uses the planktivorous fish *Alosa chrysochloris* (Raf.), the skipjack herring, as its glochidial host.

It is possible, however, that for some species of Unionidae, proliferation by *Corbicula* may exert a neutral or even a beneficial effect. In such a situation mollusk-eating fishes would probably switch their feeding preferences to *Corbicula* because such switching to a newly dominant food source is commonplace in fishes which feed by sight. Such fishes would no longer function as important predators on juvenile unionids, except for those unionid species whose surface-dwelling, post-mesoconch young resemble *Corbicula*, and a much larger proportion of juvenile unionids would survive to adulthood. Populations of such mollusk-eating fishes would also be likely to increase, and if those fishes are also hosts for indigenous mussel species, the survival chances for their glochidia would also be substantially increased. Just such a feeding shift and population increase in the molluscivorous freshwater drum or sheepshead *Aplodinotus grunniens* (Raf.), (discussed below) was observed to take place in Kentucky Lake in the lower Tennessee River soon after *Corbicula* first became abundant there (J. Bates, pers. comm.). *Corbicula*-induced ecosystem shifts, as we have mentioned, may also reduce the standing crops of carnivorous benthic insects thus also facilitating the survival of a larger proportion of postlarval juvenile mussels. Finally, if these unionid species are able to feed upon algae of larger body size than that which can be consumed by Corbicula, and the unionids occurred in deeper depths than those inhabited by Corbicula thus avoiding spatial competition, such unionids might truly thrive.

Corbicula-unionid communities which are in accord with both of the theoretical models described above have already been discussed. For example, the St. Francis Floodway in Arkansas is a river of high productivity, with large molluscan populations including long-established but now rather sparse Corbicula colonies, and abundant molluscivorous fishes. The freshwater drum or sheepshead, which feeds heavily on Corbicula where they are sufficiently available, is common there, and it is known to be the glochidial host for 11 species of unionids. Other common fishes there which almost certainly feed on Corbicula include the bluegill sunfish Lepomis macrochirus Raf., known to be a host for 13 unionid species, and the channel catfish, Ictalurus punctatus (Raf.), implicated as the host for 3 species. Although our knowledge of unionid-fish interrelationships is still incomplete, if one were to list all of the species of mussels for which the freshwater drum, bluegill sunfish, and channel catfish are known to function as hosts (see list provided by Fuller, 1974) it would be seen that 5 of the 6 most abundant mussel species in the St. Francis River, and numerous other species which are common there, are already accounted for. Further, in most of the cases where an abundant mussel does not appear to be related to a molluscivorous fish (e.g. Potamilus capax) in reality the fish host is still unknown.

Although comparative abundance data for fishes are not available, if classical predator-prey cycles occur in that community, it is possible that the fishes cited above may have become more abundant in response to, and following, a previous peak in Corbicula abundance, and that this enhanced availability of suitable fish hosts for these 5 mussel species, coupled with shifts in feeding by fishes from juvenile unionids to Corbicula, may be partially responsible for the present dominance of those mussel species.

An example of close agreement with the theoretical model for a low to moderate productivity water body has also been described above. It is the lower James River a few miles above Richmond, Virginia. Corbicula is concentrated in 2 wide bands, one on each side of the river, from depths of about 0.2 to 2 meters. Beyond these bands , at depths of about 2.5 to 4 meters, 2 dense beds containing only Elliptio complanata occur. Those unionids show unusual variability in regard to the papillae surrounding their incurrent openings, some having numerous papillae, some having few, and some having virtually none at all. This is in agreement with the conclusions of Davis and Fuller (1981) that E. complanata has greater genetic variability than any other species in the Atlantic Coastal Drainage. Only 1 glochidial host for E complanata has been identified, the yellow perch, Perca flavescens L, a species which feeds on mollusks under some circumstances (Baker, 1916), but other fishes, which may be more abundant in the James River than P flavescens, may also function as hosts. It is possible that a burgeoning Corbicula population in the James River may have resulted in a population increase for 1 or more Corbicula-eating fishes which are the hosts for E. complanata, and that this increased availability of glochidial fish hosts has substantially benefited the E. complanata population.

CONCLUSIONS

Available information, although inadequate for many purposes, is sufficiently extensive to enable some generalizations to be proposed. These are as follows :

(1) Within about 1 to 5 years after Corbicula is first introduced to a previously unoccupied, limnologically suitable, water body, its population are likely to increase dramatically and to reach densities, in many areas, exceeding 1000/m^2. This appears to be true in the Ohio-Mississippi and the Atlantic Drainages at least, and probably obtains in

the Gulf of Mexico and Pacific Drainages also. This population peak is followed by a decrease which is sudden in some water bodies and may be gradual in others. After about 12 years in some river systems of the Ohio-Mississippi Drainage, Corbicula populations may become so sparse that individuals are difficult to find, but it is uncertain whether this is a permanent or a transitory condition. Some evidence indicates that a second population peak may occur about 20 years after initial introduction in some rivers.

(2) In some Atlantic Drainage river systems Corbicula populations appear to have caused the local extinction of some species of unionids. Only one species there, Elliptio complanata, appears to be unaffected by Corbicula, and this is believed to have been made possible by the unusually great genetic variability of E. complanata. One aspect of this variability may involve the ability of some adult individuals to utilize large-bodied algal species for food which cannot be utilized by Corbicula.

(3) In Ohio-Mississippi Drainage river systems, with few exceptions, Corbicula does not appear to threaten the existence of unionid species. Elliptio crassidens may be such an exception. Data are insufficient to determine whether some areas may have suffered short-term species losses which were replenished by subsequent immigrations or not, but long-term harmful effects by Corbicula on most unionids are not evident. Other species-specific biotic attributes, e.g. the use by some unionids of fish hosts which will feed on Corbicula, may also be involved in the differences in stasis which exist between the 2 drainage areas.

(4) Because of their small sizes, many Atlantic Drainage river systems may be in danger of becoming totally dominated by dense Corbicula populations before natural reductions, sufficient to allow some species of unionids to coexist with them, have had time to occur. In such situations, all populations of these endemic unionids might be so heavily impacted that no propagules might survive for possible subsequent recovery of the species, Species believed to be in such imminent danger are Canthyria

collina (Conrad) in the James River and C. steinstansana (Johnson & Clarke) in the Tar River System. Subsequent survival of those 2 species, and especially of C. steinstansana, can be assured only if numerous living individuals are promptly removed to other water bodies and the species are cultured artificially. If ecological conditions again become suitable for their healthy existence in their native habitats they could then be reintroduced to those original river systems.

(5) The ecosystem approach, in which the interactions between and among all constituent species are considered, is closer to reality and offers a better prospect for attaining insight into Corbicula-unionid relationships than other approaches. It has already revealed likely explanations for some of the apparently contrasting relationships of these groups in the Ohio-Mississippi and Atlantic Coastal Drainages.

(6) There is a remarkable lack of information about population changes in aquatic communities over extended periods after Corbicula is first introduced. Unfortunately there are few limnologically suitable river systems now left into which Corbicula has not penetrated, but there are some. These include tributaries of the Red River in Oklahoma and Texas and tributaries of the Missouri River, as well as some streams in the Atlantic Drainage System. Students are urged to utilize these rare opportunities to study communities over extended periods beginning prior to invasion by Corbicula during the few years left while such opportunities still exist.

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Some Fresh-water Mussels from the Red River Drainage, Kentucky

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INTRODUCTION

Houp (1980) called attention to the meager knowledge of the mussel fauna of the Red River, a major tributary of the Kentucky River, in east central Kentucky. He stated, "The published data available for the Red River is limited to a fish survey by Branson and Blatch (1974), that included water quality data and information on the geology of the drainage". Although Williams (1969) survey the mussel fauna of the Kentucky River mainstream together with the North, Middle and South Forks, the Red River was not included.

When the U. S. Corps of Engineers recommended, in 1967, the construction of a reservoir in the Red River gorge area, the author made three collections of mussels from the area.

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The assistance of Dr. Henry van der Schalie, Curator of the University of Michigan's Division of Mollusca of the Museum of Zoology, at that time, in varifying the identifications of all specimens deposited in the Museum is gratefully acknowledged.

METHODS AND MATERIALS

One collection was made on September 30, 1974 (Table 1); and this site and another a few miles upstream were collected on October 29, 1974. Collections were made by hand with some assistance of a garden rake, and by "muddling". Each location was sampled for approximately two and one-half hours.

Specimens of the more common species were identified and counted in the field by the author; and a majority of them returned to the water. Represenatives of all species, and all of any species numbering 13 or less, were retained for future examination.

All specimens retained, except *Simpsoniconcha*, were deposited in the University of Michigan's Museum of Zoology. The *Simpsoniconcha* are in the author's collection.

DISCUSSION

Houp (1980) collected 15 species of naiads, in 1978-1979, from a portion of the Red River described by him as a 14.7 km segment of the Red River gorge, now protected under the Wild Rivers Act of 1972. The author collected at only two sites in the stream in 1974, from which he took 16 species (Table 1).

Ligumia recta and *Lampsilis fasciola* were collected by Houp (1980), but not by the author. Whereas *Pleurobema cordatum coccineum*, *Simpsoniconcha ambigua*, and *Proptera alata* were collected by the author, but not by Houp (Table 1). The small populations of these species is suggested by the limited numbers collected.

The lack of *L. fasciola* in the author's collections may be due to the late season of the year when the collections were made. The author's best success in finding this species in previous studies has bee during the spring breeding season when the lamellar flaps were extended and flowing in the current.

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Table 1. Locations of Red River Naiad Collections

Species Collected	North Fork of Red River- at Junction of State Route 77 and County Road 1069 9/20/74	Red River 500 feet down stream from mouth of Swift Camp Creek 10/29/74	North Fork of Red River at Junction of State Route 77 and County Road 1069 10/29/74	Red River, Wild River segement 14.7 km long 9/78-?/79
Amblema costata Rafinesque 1820	7		3	9
Fusconaia flava (Rafinesque 1820)	3		2	47
Tritigonia verrucosa (Rafinesque 1820)	25	1	15	17
Elliptio dilitata Rafinesque 1820		4	9	67
Pleurobema cordatum coccineum (Conrad 1836)	2			
Alasmidonta calceolus (Lea 1830)	12	8	7	18
Alasmidonta marginata Say 1819	4	2		91
Lasmigona costata (Rafinesque 1820)	40	38	34	55
Simpsoniconcha ambigua (Say 1825)	3			
Strophitus undulatus (Say 1825)	34	12	25	73
Actinonaias carinata (Barnes 1823)	2	1		13
Lampsilis fasciola Rafinesque 1820				16
Lampsilis ovata (Say 1817)	15			27
Lampsilis radiata siliquoidea (Barnes 1823)	18	1	18	37
Ligumia recta (Rafinesque 1820)				4
Obovaria subrotunda (Rafinesque 1820)	6		1	9
Proptera alata (Say 1817)			1	
Ptychobranchus fasciolare (Rafinesque 1820	4	5	4	34

NOTICE. In accord with the conservation orientation of this journal, the Editor welcomes reports which describe significant molluscan faunas as they were prior to anthropogenic disturbances and other catastrophic events. Such accounts provide, among other things, standards by which we can measure the success of restorative programs.

ERRATA: Regrettably, the cover of the previous issue, Vol.2, NO. 1/2, was mistakenly labelled as Vol. 2, No. 1. Papers within that issue, however, were properly identified as contained within Vol.2, No. 1/2.

Further, the paper by Lemche and Wingstrand, containewd therein, had been retrieved from our file and published without knowledge of a recent major paper by Dr. Wingstrand. It has now become available to us. It is as follows: Wingstrand, K.G., 1985. On the Anatomy and Relationships of the Recent Monoplacophora. Galathea Report, 16: 7-94, 12 pls.

INFORMATION FOR CONTRIBUTORS

Malacology Data Net (Ecosearch Series) seeks to enhance progress in malacology by facilitating rapid publication of significant new information about all aspects of marine, freshwater, and terrestrial mollusks. All scholarly contributions are welcome, but manuscripts dealing with timely issues such as current threats to the survival of molluscan species or communities, descriptions of new taxa, opportunities for participation in ongoing research programs, etc. are particularly appropriate.

Editorial style used in this journal follows the Style Manual for Biological Journals available from the American Institute of Biological Sciences, 1401 Wilson Boulevard, Arlington, VA. 22209. Manuscripts should be submitted (in duplicate) as camera ready copy, using "letter quality" type, with text in blocks 5 inches wide and 6½ inches high. Use of a word processor is recommended. Each manuscript will be reviewed by at least two professional malacologists and, if necessary, will be returned to the author for revision. After final acceptance publication will proceed rapidly, normally within about 8 weeks.

Although Malacology Data Net is without grant or institutional support no author page charges to subscribers will be assessed. If half-tone illustrations (i.e. photographs) are included in the manuscript, however, authors will be charged at cost for plate preparation and reproduction.