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Distribution of pulmonate snails in the New River of Virginia and North Carolina, U.S.A.: interaction between alkalinity and stream drainage area

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SUMMARY. The distribution and abundance of five species of pulmonate snails over 87 sites in the New River seem to be related to two variables, alkalinity and drainage area of the stream. The snails were generally found in the more alkaline streams regardless of stream drainage area and in the larger streams regardless of alkalinity. Considering only the 26 sites where at least one species of the five pulmonates occurred, rank snail abundance is significantly correlated with rank alkalinity, rank drainage area, and the alkalinity/area interaction. But the correlations between abundance and both alkalinity and drainage area drop to low levels when interaction is partialled out, while the correlation between abundance and interaction remains high upon partialling out alkalinity or area. This suggests that the apparent correlation between pulmonate abundance and alkalinity is secondary and that neither alkalinity nor water chemistry variables correlated with it directly limit the distribution and abundance of pulmonates in the New River. Both alkalinity and stream drainage area may influence the abundance of pulmonate food.

Introduction

Relationships between the distribution and abundance of freshwater snails and surface geology are well established (e.g., Appleton, 1978; Russell-Hunter, 1978). Most field studies have found that freshwater snails are either restricted to areas containing limestone or dolomite, or are more abundant in such areas (Boycott, 1936; Shoup, 1943; Macan, 1950; Økland, 1969; Williams, 1970a; McKillop & Harrison, 1972; Dussart, 1976). Transplant experiments (Malone, 1965) and laboratory work (Williams, 1970b) have corroborated field observations for particular snail species. Other macro-invertebrates, for example crustaceans, also seem to be more common and diverse in hard water (Sutcliffe, 1972).

Many explanations have been proposed for the relationship between surface geology and freshwater snail distribution, most of which focus on the direct effects of water chemistry on metabolism. Calcium concentration, water hardness, pH, alkalinity and total dissolved solids are all highly intercorrelated (Sepkoski & Rex, 1974) and all increase when rivers flow through limestone or dolomite. The absence of many snail species from soft water may be related to an inability to obtain sufficient calcium for shell construction. Another possibility is that low concentrations of ions in general make osmotic regulation difficult. Various species of freshwater snails may have minimum pH tolerances, or perhaps are unable to cope with the fluctuations in pH that are common in waters of low buffering capacity.

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In a 1976 survey of molluscs in the upper New River of Virginia and North Carolina, it was observed that the distribution and abundance of most pulmonate snail species did not seem to be a simple function of surface geology. Both the amount of limestone drained by a stream and the stream's size seemed to be involved. The purpose of this paper is to present evidence suggesting that the distribution of pulmonate snails in an Appalachian Mountain river catchment is a function of the interaction between alkalinity and stream drainage area, and to discuss possible implications of that interaction.

Methods

The upper New River drains a mountainous 7117 km^2 area in southwestern Virginia and northwestern North Carolina, U.S.A. Although geologically complex, upstream portions of the catchment are generally underlain by gneiss and schist, and downstream areas by limestone and dolomite (Fig. 1). Eighty-seven sites were selected throughout the catchment as a geographically representative sample. (Locality data for these sites are available from the first author upon request.) At each site, a team of collectors thoroughly searched the area for molluscs and scored each species by abundance. A score of 1 was assigned to uncommon species represented by a few scattered individuals. Species represented by more than a few individuals but still estimated to have less than 5 individuals per m^2 of suitable habitat were given a score of 2. An abundance score of 3 was given to species with an estimated density of greater than 5 individuals per m^2 of suitable habitat. All sites were originally visited in the spring of 1976 and were revisited at least once each spring or summer in 1977–1979. Although most pulmonate populations appeared to remain stable over the period, some revision of abundance estimates was necessary. Thus some abundances reported here are modes for observations made over several visits.

A measure of overall pulmonate abundance at each site was obtained by summing abundance values for all pulmonate species present. (The limpet, *Ferrissia,* was excluded from this study for reasons to be outlined later.) Stream drainage area at each site was estimated from a stream gazeteer (Kanawha River Basin Coordinating Committee, 1971) and topographic maps.

Values for mean total alkalinity at some sites were taken from Benfield & Cairns (1974). For the remaining sites, total alkalinity was measured at the riverbank in July, 1978. A water sample of 100 ml was first titrated to pH 8.3 using standardized 0.02N sulfuric acid and phenolphthalein as indicator. Titration was continued to pH 4.5 using methyl purple as indicator. Total alkalinity in mg 1^{-1} $CaCO_3$ was taken as ten times the volume of the acid titrant (American Public Health Association *et al.*, 1976). This figure was subsequently converted to m-equiv. 1^{-1}.

Kendall rank correlation coefficients were calculated for all pairs of four variables: abundance, alkalinity, drainage area and the interaction between alkalinity and drainage area (Siegel, 1956). The interaction term was obtained by multiplying rank alkalinity by rank drainage area and re-ordering the product. All correlation coefficients were corrected for ties. Kendall partial rank correlation coefficients were calculated between abundance and each of the three environmental variables, holding a second environmental variable constant (Siegel, 1956).

Results

Pulmonate snails (excluding *Ferrissia*) were found at 26 of the 87 sites (Fig. 1). The five species collected and values for alkalinity and drainage area at each site are listed in Table 1. Most of the pulmonates were broadly distributed throughout the New River basin. The only exception was *Physa pomilia* (Conrad), a rare species in the study area, which appeared to be restricted to sites not occupied by *Physa hendersoni* Clench. Figure 2 shows the distribution and abundance of *Physa,* the most widespread pulmonate genus in the area, plotted on the two environmental variables using a log scale. The snails were generally found in small streams only when the alkalinity was high and in low alkalinity water only when the stream was large. Occasionally, *Physa* was found in very soft water. For example, *Physa* was very common at site S, where the calcium concentration was 3.6 mg 1^{-1}, hardness was 14.1 mg 1^{-1}, total dissolved

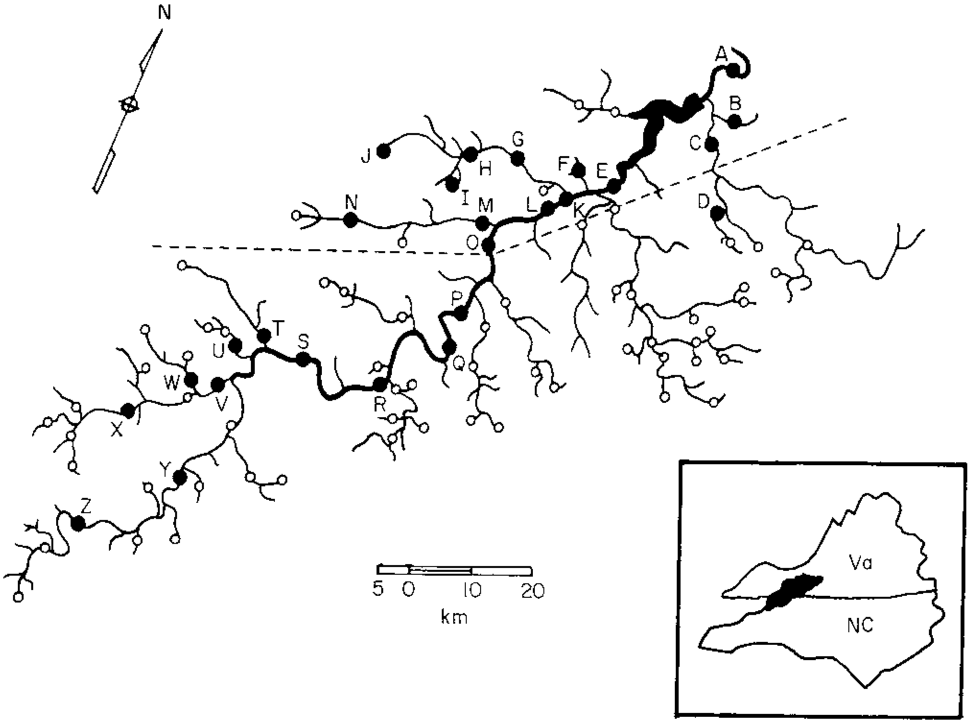

FIG. 1. Map of the upper New River showing sample sites. Darkened circles locate sites where pulmonate snails (excluding *Ferrissia*) were collected. Areas north of the dashed line are generally underlain by limestone and dolomite. Areas south of the line are principally underlain by gneiss and schist.

solids were 76.2 mg l^{-1}, alkalinity was 0.33 m-equiv. l^{-1}, and pH was 6.76 (means of 60 samples taken over a 4-year period by Benfield & Cairns, 1974). Though the other pulmonate species were less common than *Physa*, their distributions throughout the 87 sites were similar (Table 1).

Table 2 shows the simple Kendall rank correlations between all pairs of the four variables. Pulmonate abundance is highly correlated ($P < 0.01$) with the interaction between drainage area and alkalinity. Abundance is also significantly correlated with both alkalinity and drainage area individually, even though these two variables are negatively correlated with one another. Table 3 shows that the correlation between abundance and interaction remains large even when alkalinity or area is partialled out. (Unfortunately, the significance of Kendall partial rank correlation coefficients cannot be tested.) However, when interaction is partialled out, the correlation between abundance and alkalinity drops to a low level. The correlation between abundance and drainage area also drops a great deal when the effect of interaction is removed. This suggests that the true correlation is between pulmonate abundance and the alkalinity/drainage area interaction. The apparent relationships between pulmonate abundance and alkalinity or drainage area individually shown in Table 2 are secondary.

Discussion

In the upper New River, populations of several pulmonate snail species do not seem to have any absolute boundaries corresponding to particular alkalinities. Rather, the minimum alkalinity required seems to depend on stream drainage area. The snails were found commonly in large softwater rivers but not in small streams of similar alkalinity. Given that pulmonates are found at a site, there is evidence that the interaction between stream drainage area and alkalinity accounts better for the variance in pulmonate abundance than does either variable alone.

TABLE 1. Abundance (on a scale of 1–3) of five pulmonate snail species and values of alkalinity (m-equiv. l^{-1}) and drainage area (km^2)

Site	Alkalinity	Drainage area	*Physa hendersoni* Clench	*Physa pomilia* (Conrad)	*Fossaria obrussa* (Say)	*Pseudo-succinea columella* (Say)	*Helisoma anceps* Menke	Total pulmonate abundance
A	0.78**	6216		3	2		2	7
B	1.50	65		3	3		2	8
C	0.64	829		3	2	1		6
D	0.14	52			1			1
E	0.56	4921	2		1		2	5
F	1.88	26	2					2
G	1.20	518	3		3	1	2	9
H	1.38	453	3				2	5
I	1.42	91	3		1			4
J	1.60	26	2		1		1	4
K	0.68	4274	2		1			3
L	0.70**	4144	3		3			6
M	1.40	430	3		1		3	7
N	1.26	130	3		1			4
O	0.20	3497	3				1	4
P	0.36**	2849	3			2		5
Q	0.34	2720	2			1		3
R	0.34	2124	2					2
S	0.32**	1865	3		2	1	2	8
T	0.34*	158					1	1
U	0.34*	93					1	1
V	0.22	699	3		2		3	8
W	0.50	181	1					1
X	0.38**	466	2		1		1	4
Y	0.32**	622	1				1	2
Z	0.18	285	2		1			3

*Mean of twelve samples taken in 1974.
**Mean of sixty samples taken in 1970–1974.

Our results are quite similar to those obtained by Lassen (1975) and Aho (1978a,b,c) working with the snail fauna of Scandinavian lakes. They demonstrated that both lake trophic status (including concentrations of mineral salts like calcium) and lake size are required to make an accurate prediction about gastropod diversity and abundance. Both authors suggested that the number of species present in Scandinavian lakes is determined by invasion–extinction equilibria, and that smaller lakes had fewer species because extinction was more likely and invasion more difficult. The sites we studied are all well-connected and are in no sense islands. Further, the upper New River is thought to be a remnant of the ancient Teays River system and may be one of the oldest rivers in North America (Janssen, 1953; Ross, 1969). Yet a species–area relationship seems to persist.

The presence of a significant interaction between alkalinity and stream drainage area is not compatible with the hypothesis that alkalinity or its correlates directly limit pulmonate distribution and abundance in New River. We suggest that both increased alkalinity and large drainage area may have the effect of increasing food supply for pulmonate snails in the upper New River, and that the distribution and abundance of the snails may be a function of food supply. This is not an entirely new suggestion. Many authors have observed that freshwater snails are more common and diverse in eutrophic lakes than in oligotrophic lakes (Russell-Hunter, 1978), suggesting that food availability may be

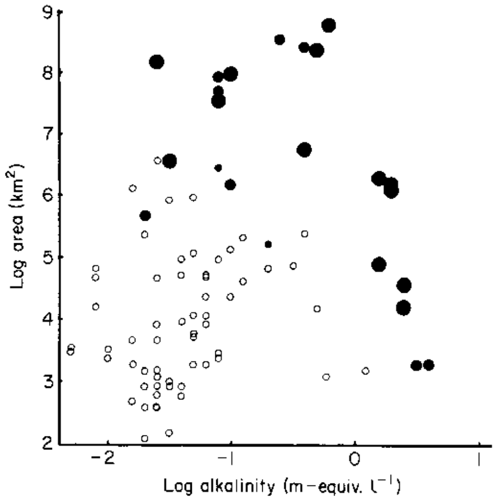

FIG. 2. The abundance of *Physa* (two species) at sites of varying alkalinity and drainage area. Small, medium, and large closed circles show sites where *Physa* had an abundance of one, two, and three, respectively. No *Physa* were collected at sites marked by an open circle.

TABLE 2. Kendall rank correlations

	Alkalinity	Drainage area	Interaction
Abundance	0.24*	0.24*	0.35**
Alkalinity	—	−0.20*	0.27*
Drainage area	—	—	0.53**

*Significant at 0.05 level (one-tailed).
**Significant at 0.01 level (one-tailed).

responsible. Eisenberg (1966, 1970) found that wild populations of *Lymnaea elodes* enclosed by pens underwent rapid growth when provided with large quantities of spinach as food. This suggests that population density was not a function of maintenance costs like osmoregulation and calcium transport, but was due to availability of food.

The dietary requirements of freshwater pulmonates are not well known. Pennack (1978) stated that most freshwater gastropods are normally vegetarians and feed on algae, but dead plant material and occasionally dead animal material is eaten by some species. He considers *Physa* and *Lymnaea* to be omnivores. Pip & Stewart (1976) found that the peak abundance of *Lymnaea stagnalis* and *Physa gyrina* on two macrophyte species correspond to peaks in the nutritive value of the plants. This suggests that the snails were either feeding on the macrophytes directly or grazing on micro-organisms colonizing the macrophytes. McMahon, Hunter & Russell-Hunter (1974) have suggested that the nutritional quality of macrophytes is generally too low to support aquatic snails. McMahon *et al.* (1974) report a relationship between the growth rates and fecundities of two pulmonates, *Lymnaea* and *Laevapex* and the C/N ratios of the Aufwuchs the snails graze upon. Calow (1970) showed that *Lymnae pereger* grazes on epiphytic algae without eating the macrophyte hosts. Calow (1973, 1974) found that *Planorbis contortus* feeds on detritus rather than algae and prefers unsterilized detritus over sterilized detritus. Available information suggests that the diets of freshwater pulmonates vary greatly and may include algae, macrophytes, detritus and associated micro-organisms.

Although there are no specific data available for the upper New River, autochthonous primary production in low-order woodland streams is usually quite low throughout most of the year, primarily due to shading. Minshall (1978) compared annual primary production rates for open and closed canopy streams in deciduous forests and found that productivity in streams with an open canopy was significantly higher than in streams with a closed canopy. The river continuum hypothesis (Vannote *et al.*, 1980) holds that as streams become larger and less shaded, periphyton production tends to increase. This trend should continue until the river deepens to the point where sunlight reaches only a small fraction of the bottom. Broad, shallow riffles remain common in the New River as far downstream as was covered by this study. (No

TABLE 3. Kendall partial rank correlations

	Alkalinity	Drainage	Interaction
Abundance correlated with:			
Alkalinity	—	0.30	0.16
Drainage	0.30	—	0.07
Interaction	0.31	0.27	—

samples were taken in the Claytor Lake impoundment between sites A and E.) Thus, periphyton production, probably an important food source for pulmonate snails, should increase as drainage area increases.

Stream alkalinity may also be involved in limiting algal growth in the relatively soft, low-order streams of the upper New River. Blum (1956) reported that neutral or slightly alkaline conditions appear to be a prerequisite for the majority of lotic algal species and that waters rich in lime, other things being equal, tend to be rich in algae. Butcher (1946) found greater numbers of algae on slides suspended on two hardwater rivers than on slides suspended for an equal length of time in several softwater streams. Marker (1976) reported that algal biomass was much greater in a hardwater stream than in either of two softwater streams throughout most of the year. Hornick, Webster & Benfield (1981) found that annual periphyton primary production was about two times higher in a slightly alkaline stream than in a naturally acidic stream in the same montaine watershed in Virginia.

If we assume that the pulmonate species in question depend largely on periphyton as a food source, and that the general patterns of periphyton production with respect to stream size and alkalinity discussed above apply to streams in the study area, a case for food limitation seems reasonable. On the other hand, if the several pulmonate species are mainly detritivores or omnivores, our food limitation hypothesis seems less likely [though Egglishaw (1968) has shown that detrital decomposition in streams increases with their calcium concentrations]. Other factors that might directly influence the distribution of pulmonates include pH, ionic concentration (specific conductance), specific ions, dissolved oxygen, toxic wastes, temperature, and substrate (Harman, 1974). In the upper New River catchment there is a gradual trend of increasing pH and specific conductance from headwater and side tributaries to the main stream, and in the downstream direction in the main stream, but major differences in either factor, or in a series of other water quality variables, are not apparent (Benfield & Cairns, 1974). The minimum naturally occurring pH over 3 years was 6.2 with means ranging from 6.5 to 8.5. Dissolved oxygen concentration remains at or near saturation levels throughout the drainage. There are a few industrial sites from which toxic wastes may originate, but the sites are widely dispersed and do not appear to constitute a general hazard. While temperature and substrate (see review by Harman, 1974) may well be important factors influencing pulmonate distribution in the study area, we have little specific data to support that hypothesis. Maximum summer temperatures may be up to 7°C cooler in some tributaries than river maxima (30°C), but minimum temperatures are about the same throughout the catchment. Substrate tends to be very similar throughout the main stream and larger tributaries in the study area but changes significantly in low-order streams (Benfield & Cairns, 1974). The general absence of the pulmonates from low-order streams (Fig. 2) regardless of alkalinity may be due to a number of factors including temperature and substrate.

It should be emphasized that not all species of freshwater snails in the New River have distributions corresponding to those of the five pulmonates discussed. In particular the limpet *Ferrissia rivularis* (Say) is the most widespread gastropod in the study area, and its distribution does not seem to reflect any preference for alkaline water. Four pleurocerid snails (Prosobranchia) common in the upper New River also seem to have different distributions from the pulmonates. *Mudalia dilatata* (Conrad) inhabits the main river and most of the larger tributaries without apparent regard for alkalinity or its correlates. *Goniobasis proxima* (Say) lives only in small tributaries with low alkalinity, and *Goniobasis semicarinata* (Say) and *G. simplex* (Say) inhabit small, high alkalinity tributaries (Dillon & Davis, 1980).

In summary, it is difficult to make generalizations about the distribution of gastropods in the upper New River. *Ferressia rivularis* and *Mudalia dilatata* appear to be generalists with respect to habitat selection while the several species of *Goniobasis* are specialists. The five pulmonate species appear to fall somewhere between the two extremes. The variability in distribution at the familial and generic levels within a single drainage area suggests that even more variation should be expected in attempts to examine factors influencing riverine gastropod distributions on a regional or continental scale. Further, our data suggest that single factor analyses are unlikely to provide sufficient explanation for the distribution patterns of riverine gastropods.

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References

Aho J. (1978a) Freshwater snail populations and the equilibrium theory of island biogeography. I. A case study in southern Finland. *Annales Zoologici Fennici,* **15,** 146–154.

Aho J. (1978b) Freshwater snail populations and the equilibrium theory of island biogeography. II. Relative importance of chemical and spatial variables. *Annales Zoologici Fennici,* **15,** 155–164.

Aho J. (1978c) Freshwater snail populations and the equilibrium theory of island biogeography. III. An explanation for the small number of species in South Bothnia, western Finland. *Annales Zoologici Fennici,* **15,** 165–176.

American Public Health Association, American Water Works Association & Water Pollution Control Federation (1976) *Standard Methods for the Examination of Water and Wastewater.* APHA, Washington, D.C., 1193p.

Appleton C.C. (1978) Review of literature on abiotic factors influencing the distribution and life cycles of bilharziasis intermediate host snails. *Malacological Review,* **11,** 1–25.

Benfield E.F. & Cairns J. (1974) *A three year report. Pre-impoundment ecological reconnaissance of the New River in the area of the proposed Appalachian Power Company's Blue Ridge Project.* Virginia Polytechnic Inst. and State U., Blacksburg, 1974.

Blum J.L. (1956) The ecology of river algae. *Botanical Review,* **22,** 291–341.

Boycott A.E. (1936) The habitats of freshwater mollusks in Britain. *Journal of Animal Ecology,* **5,** 118–186.

Butcher R.W. (1946) Studies in the ecology of rivers. VI. The algal growth in certain highly calcareous streams. *Journal of Ecology,* **33,** 268–283.

Calow P. (1970) Studies on the natural diet of *Lymnaea pereger obtusa* (Kobelt) and its possible ecological implications. *Proceedings of the Malacological Society of London,* **39,** 203–215.

Calow P. (1973) Field observations and laboratory experiments on the general food requirements of two species of freshwater snails, *Planorbis contortus* (Linn.) and *Ancylus fluviatilis* Mull., *Proceedings of the Malacological Society of London,* **40,** 438–489.

Calow P. (1974) Evidence for bacterial feeding in *Planorbis contortus* (Linn.) (Gastropoda: Pulmonata). *Proceedings of the Malacological Society of London,* **41,** 146–156.

Dillon R.T., Jr & Davis G.M. (1980) The *Goniobasis* of southern Virginia and northwestern North Carolina: Genetic and shell morphometric relationships. *Malacologia,* **20,** 83–98.

Dussart G.B.J. (1976) The ecology of freshwater molluscs in North West England in relation to water chemistry. *Journal of Molluscan Studies,* **42,** 181–198.

Egglishaw H.J. (1968) The quantitative relationship between bottom fauna and plant detritus in streams of different calcium concentrations. *Journal of Applied Ecology,* **5,** 731–740.

Eisenberg R.M. (1966) The regulation of density in a natural population of the pond snail, *Lymnaea elodes. Ecology,* **47,** 889–906.

Eisenberg, R.M. (1970) The role of food in the regulation of the pond snail, *Lymnaea elodes. Ecology,* **51,** 680–684.

Harman W.N. (1974) Snails (Mollusca: Gastropoda). In: *Pollution Ecology of Freshwater Invertebrates,* (Eds C. W. Hart & S. L. H. Fuller), p. 275–312.

Hornick L.E., Webster J.R. & Benfield E.F. (1981) Periphyton production in an Appalachian Mountain trout stream. *American Midland Naturalist,* (in press).

Janssen R.E. (1953) The Teays River, ancient precursor of the east. *Scientific Monthly,* **Dec,** 306–314.

Kanawha River Basin Coordinating Committee (1971) Hydrology. In: *Kanawha River Comprehensive Basin Study, Vol. III.* U.S. Army Corps of Engineers, Huntington, W.Va.

Lassen H.H. (1975) The diversity of freshwater snails in view of the equilibrium theory of island biogeography. *Oecologia (Berl.),* **19,** 1–8.

Macan T.T. (1950) Ecology of freshwater mollusca in the English Lake District. *Journal of Animal Ecology,* **19,** 124–146.

Malone C.R. (1965) Transplant studies with *Physa anatina* Lea (Gastropoda) in Andrews County, Texas. *American Midland Naturalist,* **74,** 325–328.

Marker A.F.H. (1976) The benthic algae of some streams in southern England. I. Biomass of the epithon in some small streams. *Journal of Ecology,* **64,** 343–358.

McKillop W.B. & Harrison A.D. (1972) Distribution of aquatic gastropods across an interface between the Canadian shield and limestone formations. *Canadian Journal of Zoology,* **50,** 1433–1445.

McMahon R.F., Hunter R.D. & Russell-Hunter W.D. (1974) Variation in *Aufwuchs* at six freshwater habitats in terms of carbon biomass and of carbon: nitrogen ratio. *Hydrobiologia,* **45,** 391–404.

Minshall G.W. (1978) Autotrophy in stream ecosystems. *BioScience,* **28,** 767–771.

Økland J. (1969) Distribution & ecology of the freshwater snails (Gastropoda) of Norway. *Malacologia,* **9,** 143–151.

Pennack R.W. (1978) *Freshwater Invertebrates of the United States. Second Edition.* John Wiley and Sons, New York. 803 p.

Pip E. & Stewart J.M. (1976) The dynamics of two aquatic plant-snail associations. *Canadian Journal of Zoology,* **54,** 1192–1205.

Ross R.D. (1969) Drainage evolution and fish distribution problems in the southern Appalachians of Virginia. In: *The Distributional History of the Biota of the Southern Appalachians, Vol. I* (Ed. P. C. Holt), pp. 277–292. Virginia Polytechnic Institute and State University Research Division Monograph I., Blacksburg.

Russell-Hunter W.D. (1978) Ecology of freshwater pulmonates. In: *Pulmonates, Vol. 2A,* (Eds V. Fretter & J. Peake), pp. 335–383. Academic Press, New York.

Sepkoski J.J., Jr & Rex M.A. (1974) The distribution of freshwater mussels: coastal rivers as biogeographic islands. *Systematic Zoology,* **23,** 165–188.

Shoup C.S. (1943) Distribution of freshwater gastropods in relation to total alkalinity of streams. *Nautilus,* **56,** 130–134.

Siegel S. (1956) *Nonparametric Statistics for the Behavioral Sciences.* McGraw-Hill, New York. 312 p.

Sutcliffe D.W. (1972) Notes on the chemistry and fauna of waterbodies in Northumberland, with special emphasis on the distribution of *Gammarus pulex* (L.), *G. lacustris* Sars and *Asellus communis* Say (new to Britain). *Transactions of the Natural History Society of Northumberland, Durham, & Newcastle Upon Tyne,* **17,** 222–248.

Vannote R.L., Minshall G.W., Cummins K.W., Sedell J.R. & Cushings C.E. (1980) The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences,* **37,** 130–137.

Williams N.V. (1970a) Studies on aquatic pulmonate snails in central Africa. I. Field distribution in relation to water chemistry. *Malacologia,* **10,** 153–164.

Williams N.V. (1970b) Studies on aquatic pulmonate snails in central Africa. II. Experimental investigation of field distribution patterns. *Malacologia,* **10,** 165–180.

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