Ruth Patrick

Benthic Stream Communities

A discussion of the factors that affect their structure and how they function

Stream shores and beds typically provide many diverse habitats for life because they include the water and bed substrates through which organisms move, the stems and leaves of rooted aquatic plants, and the debris that settles out of the water. Such diversity facilitates the development of many niches for different species. Those organisms like protozoa that live in these habitats, either attached to plants, animals, debris, or inorganic substrates or floating or swimming in the water close to the bed of a stream, are referred to as benthic organisms, and the communities they form as benthic communities.

A community is usually thought of as a group of organisms that interact. In a stream, there are typically many small compact communities, and also larger, more loosely formed communities—for example, estuarine fish that swim upstream to the headwaters to spawn and rear their young. Similarly, in the phenomenon of downstream drift, organisms born in headwaters spend most of their lives at considerable distances downstream.

The question is often asked why, over time, all organisms do not end up in the estuary. There are many factors which prevent this possibility. It is often thought, for example, that storms scour populations and cause them to drift downstream. Storms do remove large numbers of individuals of various species; and some can completely wipe out whole species populations. However, in an examination of Ridley and Darby Creeks (Chester County, Pennsylvania) under flood conditions, it was found that not all individuals of the various species had suffered the above fate. As Leopold, Wolman, and Miller (1964) have shown, the current on the surface of a rock in a stream is much less than that in free-flowing water. Motile organisms find areas such as the interstitial spaces between rocks and rubble or even protected sand where currents are greatly reduced. Some diatoms actually attach themselves to the substrate by a gelatinous secretion and can thus withstand the considerable forces of water. These statements are not intended to minimize the serious effect of floods in reducing population sizes but rather to emphasize the fact that a sufficient number of individuals of a species usually remain in an area to carry on reproduction. There is a second reason why benthic organisms survive in their habitat. Many organisms, particularly crayfish and some molluscs, naturally move short distances upstream. Several observers have noted that after emergence, female and male insects perform a more or less random mating flight, sometimes moving slightly upstream, sometimes moving slightly downstream, and other times staying in the area in which they emerged. As a result of this flight, females may deposit their eggs in any one of these three areas.

The kinds and numbers of species composing a benthic community vary according to the chemical and physical conditions of the stream and to the invasion rate of the species pool capable of inhabiting a given area. Those chemical and physical characteristics of water that affect available nutrients or have nutrient value determine the size of populations which develop. For example, in an oligotrophic stream, where the nutrient level is very low, one typically finds many species with extremely small populations. It takes a longer time to sample an oligotrophic stream adequately than a highly nutrient or eutrophic stream because many species can be over-

Dr. Ruth Patrick is Curator and Chairman of the Limnology Department of the Academy of Natural Sciences. She is also an Adjunct Professor of the University of Pennsylvania. Her research has mainly concerned problems of diversity in natural and perturbed stream environments, with special emphasis on the systematics of diatoms and the structure and functioning of diatom communities. She was elected a member of the National Academy of Sciences in April 1970.
The author wishes to express her sincere thanks to Professor G. E. Hutchinson, whose critical questions and thoughtful comments have inspired much of the thinking and research work set forth in this paper.
Address: The Academy of Natural Sciences, Philadelphia, PA 19103.

looked. Mesotrophic and eutrophic streams sustain larger species populations and thus are easier to sample. Even though the biomass varies, the number of species and their relative population sizes are often quite similar in unpolluted oligotrophic, mesotrophic, and eutrophic streams. In dystrophic streams, those low in nutrients, one often finds fewer species and a much greater difference in the relative sizes of populations than in oligotrophic–to–eutrophic or harmonic streams.

Benthic communities typically consist of many species with varying life histories. For example, among the diatoms, one finds types that reproduce once a day, once in three days, once a week, or sometimes once in several weeks. Likewise, some of the aquatic insects reproduce once a year, three times a year, or even more frequently. The same is true for protozoa and other groups of organisms. The diversity in generation time for these various species is indeed great, but the total generation time for even the longest-lived species is very short compared to that of some plants and animals in land communities.

The strategies of survival that have been adopted by most of these species involve small body size, a short generation time, and a high reproductive rate. They also may have the ability to produce resting cells, spores, or eggs that survive through the winter; or they may have the ability to pupate or lower metabolic rates in order to withstand rigorous changes of environment. Clifford (1966) has shown that the isopod *Lirceus fontinalis* and the amphipod *Crangonyx forbesi* often burrow between rocks or into the substrate in order to avoid unfavorable conditions. In only a very few cases has homeostasis been adopted in stream communities as a method of meeting changing environment. Likewise the K strategy discussed by MacArthur and Wilson (1967), in which evolution favors "the efficiency of conversion of food into offspring," has rarely been utilized.

Energy and nutrient sources are quite different for benthic stream communities than for similar life in lakes or on land. In streams, nutrients, whether dissolved, suspended, or organismal, continually enter a given area from upstream or from the watershed. This constant but variable method of renewal is a more important nutrient source than the recycling of nutrients, which is so characteristic of lake and terrestrial communities. This method is of course subject to greater fluctuation and less predictability in the concentration and kinds of nutrients than obtains in the recycling process. Because of the continuous, unpredictable renewal of substances, the depletion of a given nutrient by one plant species is less likely to occur. Thus, competition for a given limited resource does not occur as often, and its subsequent effects on the structure of the community are not as evident in stream communities as in those belonging to lakes or the land. In addition, autotoxic substances are continually removed from the organism that produces them.

Benthic communities have four or five stages of energy transfer. In each community, there are decomposers, primary producers, herbivores, and primary and sometimes secondary carnivores. Omnivores, which feed on two or three of the above groups, are always present. Each of the groups of organisms performing these various functions contains a great many species representing different genera, orders, and systematic groups, with diverse life histories. The variation in kinds of organisms and in their ecological and food preferences probably gives stability to the system and insures that a given stage in the food web is not eliminated over time. Hutchinson has pointed out that diversity is an important characteristic of stable communities and that the evolution of biological communities produces aggregates of species which increase in stability (1943, 1959). MacArthur (1955) has also shown that communities with many food pathways are more stable than those with a few.

Predator-prey relationships are among the more important interactions in benthic communities. It is well known that certain organisms pass from herbivorous to carnivorous or omnivorous stages during their life histories. More recent studies have shown that not only will a given species prefer a certain type of food, such as algae, but often will be quite selective among the kinds of species available. Aquatic organisms rarely depend on a single species for their only food source; they may, however, select a single taxonomic group, such as diatoms. Gizella and Gellert (1958) have shown that certain species of ciliates eat only diatoms, while others prefer bacteria and still others take combinations of the two. In varying degrees they are generalists.

Community structure may be altered in various ways depending on the feeding habits and preferences of the predator (Brooks 1965). Recent experiments conducted by Katherine Roop in our laboratory have shown that the snail *Physa heterostropha* will feed upon most species of diatoms but will seldom eat *Cocconeis placentula*. This species is allowed to form large populations and, as a result, the diversity of the community is greatly reduced. In contrast, other types of predator pressure seem to increase diversity.

For example, we have found that blackfly larvae develop very large populations in streams when carnivorous insects such as mayflies or stoneflies are absent. If these insects are present, however, the blackfly larvae form the small-to-moderate size populations which are characteristic of most species in the community, and predator pressure increases its diversity. Paine (1966) has shown that the presence of the starfish *Pisaster* increases diversity in intertidal zones.

Another type of interaction occurs as a result of the habitat preferences of different species. Scott (1958) and, to some extent, Edington (1965) have shown that certain caddisflies (*Trichoptera*) prefer a particular current speed and will actively occupy the areas of their preference. Bovbjerg and his students discovered that caddisflies often exhibit aggressive behavior toward other species of caddisflies, or even to individuals of the same species who try to usurp their preferred habitat (Glass and Bovbjerg 1969).

Density phenomena or competition resulting from saturation of an environment with specimens and/or species have also been observed in benthic communities. For example, in diatom communities, we have found that, when small areas of glass slides become saturated with diatoms, the species containing the smallest populations become extinct. Waters (1966) has shown that, when population densities of the mayfly *Baetis vagans* reach a certain critical number, drift occurs. The initiation of this drift may be correlated with the absence of light or certain temperature changes.

The effects of density-independent factors have been discussed by Hutchinson (1953) and are of equal importance in the structure of these communities. The environment in the stream is often rigorous and changeable and, as a result, populations of species are continually being decreased. Once population sizes have been severely reduced and space is available, one or a few opportunistic species may invade the area and quickly establish large populations. This results in a rapid change in relative population size and in the species composing the community. Although many species are present, the community has a low level of equability and diversity.

Patrick and others (1949, 1961) have demonstrated that the number of species in stream communities remains relatively similar over time although the kinds of species may change greatly. This high possibility of species change at a given trophic level indicates that a large number of taxa may perform the same function in the community at different times. It follows therefore that those species best adapted to a given set of ecological conditions will be the ones performing the function at that point of time. Patrick (1949, 1961) has also shown that ecologically similar sections of different rivers or of the same river support similar numbers of species although their kinds vary greatly. As a result of their denuding experiments on islands, Simberloff and Wilson (1969) found that approximately the same number of species reestablish themselves although the kinds of species may be quite different from those extant under pre-denuding conditions. Blum (1956) and others have concluded that in any one benthic area, there is no ordered replacement of groups of species such as that characteristic of land communities. We too have observed this phenomenon although we noted some predictability in species replacement over short periods of time caused by shifts in seasonal conditions. This characteristic is made possible by the large number of short-lived species capable of invading and functioning in benthic communities.

In general, communities in nature are classified as to their degree of maturity based on their population sizes, the metabolic rates of the species they contain, the length of life cycle of the majority of the species, and the production of offspring. Young communities are defined as having species with widely fluctuating population sizes, high metabolic rates, short life cycles, and high reproductive rates, producing a large number of offspring. In contrast, mature communities are characterized by species with more stable population sizes, longer life cycles, lower metabolic rates, and fewer but more protected offspring. According to these criteria and those set forth by Hutchinson (1959), stream benthic communities are relatively immature, for they are characterized by small, rapidly reproducing species with relatively short life cycles. Their population sizes fluctuate, but are more consistent than in pioneer communities.

Most benthic species have more than one prey and, in varying degrees, are generalists. The strategic combination of many diversified species at different stages of energy transfer with many energy pathways has enabled these communities to survive in a rigorous environment. Furthermore, the strategy minimizes the value of the individual for stability of the system by having small individuals and rapid turnover rates. Stability is ensured by the existence of many species capable of performing a given function, so that one group of species can assume the function under one set of environmental conditions and be quickly replaced by another when the environment changes.

The introduction into these communities of pollutants containing nutrient enrichment or substances of very low toxicity generally causes some change in the size of the species populations present. In some cases, reproduction in some species is inhibited by the pollutant whereas others tolerate it and show increased reproductive rates. A pollutant may also act more severely on the very young or very old individuals, thus causing a shift in the relative numbers of individuals in various age classes within a single species. A higher degree of perturbation usually brings about a change in the kinds of species and the elimination of a few types. Usually those that are sensitive and specialized disappear. The generalists are more tolerant of the changed environment and are able to increase by utilizing the nutrients that were formerly divided among a greater number of species.

If a pollutant increases the level of nutrients, the tolerant species become much more abundant; if a pollutant reduces predator pressure, the increase of the tolerant species will be even greater. More intense changes, such as the introduction of highly toxic pollutants, can actually effect a severe reduction in numbers of species and in the food pathways of the community. Toxic pollution may also repress the community's reproductive capacity and thus cause a reduction of the biomass.

We have found that various kinds of pollution produce various combinations of these effects. By studying the pattern of such changes, we can usually identify the type of pollution causing the perturbation. It seems evident that the general effect of such perturbation is to reduce the diversity, complexity, and stability of the community. Just how much reduction in its characteristic diversity the aquatic environment can withstand without serious damage to its efficient functioning and stability is a problem needing research at the present time. We also need to try to learn how to supplement or alter ratios of nutrient chemicals in small, hard-to-remove pollutants so that they will maintain diversified, stable benthic communities rather than produce nuisance growths and lower water quality.

References

Blum, J. L. 1956. Application of the climax concept to algal communities of streams. *Ecology*, 37:603–04.

Brooks J. L., and S. I. Dodson. 1965. Predation, body size, and composition of plankton. *Science*, 150:28–35.

Clifford, H. F. 1966. The ecology of invertebrates in an intermittent stream. *Investigations of Indiana Lakes and Streams* 7:57–98.

Edington, J. M. 1965. The effect of water flow on populations of net-spinning Trichoptera. *Mitt. Internat. Verein. Limnol.*, 13:40–48.

Gizella, T., and J. Gellert. 1958. Uber Diatomeen and Ciliaten aus dem Aufwuchs der Ufersteine am Osturfer der Halbinsel Tihany. *Ann. Inst. Biol. Hung. Acad. Sci.* (Tihany), 25:240–50.

Glass, L. W., and R. V. Bovbjerg. 1969. Density and dispersion in laboratory populations of caddisfly larvae (Cheumatopsyche, Hydropsychidae). *Ecology*, 50:1082–84.

Hutchinson, G. E. 1943. Food, time, and culture. *Trans. New York Acad. of Sciences*, Series 2, 5:152–54.

———. 1953. The concept of pattern in ecology. *Proc. Acad. Nat. Sci. Philadelphia*, 105:1–12.

———. 1959. Homage to Santa Rosalia. *The American Naturalist*, 93:145–59.

Leopold, L. B., M. Wolman, and J. Miller. 1964. *Fluvial Processes in Geomorphology*. San Francisco: W. H. Freeman.

MacArthur, R. H. 1955. Fluctuations of animal populations and a measure of community stability. *Ecology*, 36:533–36.

MacArthur, R. H. and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton, N. J.: Princeton Univ. Press.

Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist*, 100:65–75.

Patrick, R. 1949. A proposed biological measure of stream conditions based on a survey of Conestoga Basin, Lancaster County, Pennsylvania. *Proc. Acad. Nat. Sci. Philadelphia*, 101: 277–341.

———. 1961. A study of the numbers and kinds of species found in rivers in eastern United States. *Proc. Acad. Nat. Sci. Philadelphia* 113(10):215–58.

Scott, D. 1958. Ecological studies on the Trichoptera of the River Dean, Cheshire. *Arch. Hydrobiol.*, 54:340–92.

Simberloff, D. S., and E. O. Wilson. 1969. Experimental zoogeography of islands: the colonization of empty islands. *Ecology*, 50:278–95.

Waters, T. F. 1966. Production rate, population density, and drift of a stream invertebrate. *Ecology*, 47:595–604.