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THE ECOLOGY OF RIVER ALGAE

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INTRODUCTION

While there are probably many habitats on earth which are surrounded by a fluid in more or less unidirectional motion, the peculiarities of the cross section of a stream, its seasonal habits and its linear but ramifying nature are unique. The algae which inhabit

it find themselves provided advantages and disadvantages which are not shared in the lenitic habitat. In general, the unpredictability of flowing water presents a danger which few organisms have met to complete satisfaction. The evolution of river organisms, while successful in several isolated segments of the animal and plant kingdoms, has found relatively few organisms susceptible of being molded to this difficult last. A general description of the stream habitat can be found in several recent works (143, 224, 230, 235).

ECOLOGICAL CLASSIFICATION OF RIVER ALGAE

Species of river algae largely represent (*a*) opportunists which can grow in a current as well as in standing water, or displaced forms from an upstream impoundment; a minority of species (*b*) are inhabitants uniquely of flowing water, but these may represent a greater photosynthetic output than that of group (*a*), for, specialists as they are, their growth is frequently very dense and extremely rapid. Most of the unicellular forms are plankters, or, better, facultative plankters, for many or all of them are apparently capable of growth either on the bottom or trapped within the meshes of a filamentous alga or fungus. With this reservation, river algae are thus separable into phytoplankton and benthic algae.

Euplankton organisms in streams (potamoplankton) are probably relatively few in number, most or a majority of individuals taken in a water sample being derived from the bottom (10, 42, 129) either directly or after reproduction en route. Hence the unattached forms which bear some relation to the bottom (benthoplankton) are probably in the majority, at least in smaller streams. Benthic algae comprise several life-forms. Single-celled species may grow attached to virtually any support in the water. Certain diatoms may grow en masse on rocks or silty banks, with no ostensible means of attachment save for the calcium carbonate which they deposit around themselves. Minute filamentous forms may grow parallel and more or less adherent to each other and thus form a miniature cushion or stratum on a rock or other substrate. Other species may grow epiphytically on such a stratum, or mingled with its filaments much like a space parasite. The attached filamentous algae with large macroscopic thalli grow from a holdfast and bear the same spatial relationship to the moving water as

a tree does to the air around it. Cedergrén pointed out that virtually all forms are reducible to two types, namely (a) those like *Cladophora* and *Tetraspora* with a large surface area but with great flexibility, permitting water to run through or around them, and (b) those with a greatly reduced surface but with a hard, inflexible structure such as *Gongrosira* and *Phormidium* (49). The rock substrate, especially that afforded by large rocks, permits the best growth of both these general types. Sandy bottoms are unfavorable for algal attachment, and sandy streams tend to be poor in benthic algae (49). Although certain hydrophytic and algal growth forms have been named (49, 141, 226), the benthic types have not yet been accorded complete analysis.

Of the systems of ecological classification, that of Symoens, which is based upon floristic composition, aspect, syngenetical relationships, and synecology, is perhaps the most comprehensive. It attempts to fit known fresh water algal associations within a basic pattern of eighteen alliances, at least three of which refer to running water (221).

COMPOSITION OF THE RIVER FLORA

A beginning has been made by several authors in the cataloguing of stream communities (5, 20, 21, 36, 43, 44, 81, 103, 109, 114, 124, 142, 144, 146, 162, 193, 221, 239). The plant community in an aquatic habitat remains somewhat more difficult to define than a land community because of the unstable nature of the environment, the rapid changes in component organisms, the fact that most plants involved are thallophytes, and the tendency for numerous benthic algae to cover over extensive areas in completely dominant, monospecific stands; monospecific, that is, if one leaves out of consideration minute but numerous fungi and diatoms. The work which has been done, furthermore, is yet inadequate to give any generalized picture of the vegetation of streams for the world as a whole. This inadequacy will persist until extensive specific areas of various countries have been worked out. We are thus in a position with respect to river algae similar to the position 60 or 70 years ago with respect to the terrestrial vegetation of temperate western countries. But we are not likely to have soon a well-drawn picture of the cryptogamic vegetation of streams. The number of streams on earth is enormous, and they exhibit varying

degrees of isolation and individualism. Berg (17) points out that due to the changing character of streams from source to mouth it is not possible to group watercourses ecologically, but only parts or reaches of watercourses. The more heterogeneous the ecological conditions of a body of water, furthermore, the more associations and species it may be expected to support. The boundary of each drainage basin represents a barrier to the migration of aquatic organisms and hence to the development of extensive uniform communities such as are familiar on land or in the sea. Perhaps indeed the well-drawn picture of stream vegetation will never be achieved, inasmuch as the influence of man and his works on streams becomes continually more profound, and many natural river communities may be totally obliterated by human disturbance before scientific work on them can be undertaken.

PLANKTON COMMUNITIES

The existence of plankton in streams was apparently first reported about 1892 (cf. 85). Several German rivers received early study, and confirmation was soon obtained of the existence of a plankton in streams generally. Some streams have been found which do not develop a plankton, and the environment necessary for this condition has been studied (133). Differences and similarities between the species composition of the potamoplankton and the limnoplankton (lake plankton) have received much attention. Whereas the nekton and benthos include many distinctive organisms, workers are generally agreed that no distinctive association of phytoplankton is found in streams, although there is some evidence of this for individual zooplankters and for a few individual algae and bacteria (125, 206, 216). Plankton organisms are often introduced into the current from impoundments, backwater areas or stagnant arms of the stream (10, 36, 64, 118, 133, 134, 232). The plankton which is developed in standing waters within the river's basin is, however, frequently destroyed or filtered out downstream (43, 50, 186). There are also indications that certain river plankters are unable to survive conditions of life within an impoundment (171). Rivers whose plankton is not dominated by species from upstream lakes or ponds are likely to exhibit a majority of forms which have been derived from the stream bottom directly and which are thus merely facultative or opportunistic

plankters (43). The older literature dealing with these problems has already been reviewed by Des Cilleuls (55). While there exists a number of records of the entry of benthic organisms into the potamoplankton (20, 22, 41, 43, 47), little if any work has been done on the deposition or settling out of plankton organisms on the silt of the river bed, which must be an equally important phenomenon in the biology of the stream (cf. 150).

The commoner algae found as plankters include *Asterionella formosa*, *Fragilaria capucina*, *F. crotonensis*, *Synedra ulna*, *S. acus*, *Tabellaria fenestrata*, *Melosira granulata*, *M. varians*, *Stephanodiscus hantzschii*, *Dinobryon sertularia*, and species of *Pediastrum*, *Scenedesmus*, *Closterium*, and *Euglena*. Certain potamoplankton communities have received formal names (36, 146), but demonstration is needed that these communities have more widespread occurrence.

Panknin (161) has treated the phytoplankton of a lake as a single community and does not deem the changes with season or with depth range as worthy of consideration in representing the boundaries of different communities. He finds this interpretation of the phytoplankton as a slowly changing, self-replacing community a more truly biological concept than a more rigorous one based on floristics. Probably this interpretation is equally valid when applied to the potamoplankton.

BENTHIC COMMUNITIES

Benthic algae are dominated in much of the North Temperate Zone by *Cladophora glomerata*, which grows in riffles (shallows) and in rapidly flowing water, but never in still water. Other benthic algae must often grow in competition with, or shaded by, this species. In cold streams various Rhodophyceae which approach the size of *Cladophora*, species of *Batrachospermum*, *Lemanea*, *Thorea*, and others, are to be expected. Another red alga, *Compsopogon*, is common in warm climates. *Hydrurus* is a member of the Chrysophyceae which is widespread in cold mountain streams in Europe, and is apparently much less common in North America. It has been regarded as the "Characterart" of an algal association which includes *Scytonema mirabilis* and *Rivularia* sp. as subdominants (162). All aspects of the algal vegetation may be profoundly influenced by pollution. *Cladophora* is

adversely affected by the presence of various metallic ions in the water and may under these conditions be replaced by *Stigeoclonium tenue*, *Spirogyra fluviatilis*, *Phormidium autumnale*, *Sphaerotilus natans* or other pollution-tolerant forms (20, 229). In Scandinavian streams *Cladophora* is less conspicuous than in warmer parts of Europe, being replaced by *Zygnema*, *Vaucheria* and other algae (103). There is reason to suppose that this may be true of arctic regions generally (223).

In British streams several communities of small crustose algae appear to be very widespread. These include an *Achnanthes-Chaetopeltis* community and a *Cocconeis-Ulvella-Chamaesiphon* community (44). To what extent these communities will be found in other parts of the world is a matter of considerable ecological interest. Another community of British streams, the *Phormidium-Schizothrix-Audouinella* described by Fritsch (83, 84) is a crustose association which is probably widespread in hard water streams, perhaps throughout the world. The principal blue-green components of this crust, *Schizothrix fasciculata*, *S. pulvinata* and *S. lacustris* grow on submerged rocks, forming dense tufts of radiating filaments which may be only 0.5 mm. in height. As the *Schizothrix* grows, two other species frequently invade the tufts: *Phormidium incrustatum*, whose filaments mingle with the tufts and grow, with either horizontal or vertical orientation, twisted in and out between the *Schizothrix* filaments; and *Audouinella* sp., which grows radially like the *Schizothrix* out to the limits of the tufts, where it branches while its upward growth keeps pace with, or slightly surpasses, that of the *Schizothrix* and *Phormidium* species. These four or five organisms constitute a single layer, and apparently all of them may secrete calcium carbonate abundantly, thus converting the entire tuft, or stratum of continuous tufts, into a crust (20, 83, 84, 113). This crust becomes especially stony and resistant in the presence of a dense admixture of *Phormidium incrustatum*. After growth for a year or more, the tufted layer may eventually attain a thickness of 4–5 mm. (20). Frequently, at seasons when other benthic algae are abundant within the stream, it becomes an inferior layer, shaded and more or less enveloped by temporary dominants such as *Cladophora glomerata*. At other seasons it remains the dominant plant community, a true climax society and one which controls to a greater extent than any other

species or group of species, the micro-environment of the stream bottom. This community is an outstanding example of an algal association of high constancy which is comparable to that of well-known terrestrial communities of vascular plants. Several other crustose algal communities have also been described from streams (20, 81, 114, 142).

Benthic communities of algae other than the lithophilic types discussed above include the attached diatom communities (21, 36, 41) and groupings of forms which live on submerged silt deposits (36, 74).

FACTORS INFLUENCING RIVER ALGAE

SIZE OF STREAM

Butcher (44) has concluded that as rivers become larger, certain changes in the potamoplankton can be expected; specifically that small green and blue-green algae become relatively more important in the plankton than diatoms such as *Fragilaria* and *Synedra*. Whether these changes can be regarded as successional and of general import for streams, remains to be seen. At least some small streams develop a considerable plankton population within a few miles of their headwaters (130), but for streams in general the conclusions of Eddy (69), namely, that the development of potamoplankton is dependent on the age of the water, i.e., the distance in time from the source, probably holds good. Problems of distribution of benthic algae within a river basin are discussed below under the heading "Distribution in space".

CURRENT RATE

Current rate is influenced by a number of well-known variables (140); in any small stream these variables may act in such a complex way that minute differences in position may be subjected to vastly different current pressures (20). In smaller streams, such pressures are furthermore likely to fluctuate greatly from moment to moment within a given maximum-minimum range, and over a period of a few days even this range must shift markedly in response to changes in water level. The maximum speed of the water is usually attained near the surface and decreases sharply toward the bottom (235). Berg (16) has discussed the possibility that the micro-environment of the stream bottom is surrounded by

water which is not in motion at all. It is clear that benthic algae are exposed to much less current pressure than that of the surface water, and it is probable that massive filamentous algae on the bottom enclose between their filaments a volume of water which is essentially stationary, yet is in contact on all sides with constantly renewed water which brings fresh supplies of oxygen and essential nutrients. The same may be said for any alga which inhabits the area immediately downstream from large rocks or other prominences within the stream. Here there is little water movement save for gentle flushing from all sides, yet there is no question but that this situation is one of the most favorable in a stream as regards plant growth, for the algae there grow more rapidly and frequently more massively than in any other situation within the stream. The fact that algae colonize so dangerous a habitat as flowing water suggests that they can be provided something unique in this habitat (45, 49). It is noteworthy in this connection that flowing water can permit even in summer the growth of species which thrive in stagnant water only in late spring or early fall (49).

It is commonly observed that only certain algae will grow in rapid water, and that usually these will grow much more luxuriantly where the current is very rapid than where there is little current. On careful observation it is often found, indeed, that a projecting ledge of rock effectively shields the thallus from the full force of the current. The explanation for the improved growth in rapid water has proven elusive, however. In a comparison of more rapid parts of a riffle which supported growth of *Cladophora*, with quieter parts of the same riffle where no *Cladophora* was to be found, no significant difference in dissolved oxygen during day or night was detected (20). When the riffle was compared with deeper, quieter water immediately adjacent, the concentration of dissolved oxygen in the riffle was distinctly higher at night than in the pool. Comparisons between riffle and pool conditions as regards inorganic phosphate content indicate that minutely larger amounts are present in the faster water of riffles (author, unpublished). However, it has not been demonstrated that such small differences are sufficient to account for the incomparably better growth in waters of the riffle, nor that the increased nutrients are not actually the result, instead of cause, of the improved algal

growth there. Neel (154) has stated that greater consumption of nutrients occurs in rapids than in pools, but this would appear to depend on the density and nature of the biota of the respective habitats. For Brazilian waters, for example, it has been concluded (92) that rapid streams are less productive than large, slow-flowing rivers, and that the rapids themselves are less productive than quiet portions. Work on black-fly larvae (241) indicates that the preference exhibited for rapid waters is a response to current itself, not to oxygen demand, and there is much to indicate that the same may be true for the algae of rapids. Acceptance of this idea, however, would merely relegate an adequate explanation to one or the other of the numerous factors which, like dissolved oxygen (108), are controlled or influenced by current rate. As Butcher (44) has stated, there is clearly some physical difference between still and running water connected simply with movement.

In regions of relatively fast flow, thallus size of *Rivularia hemitites*, a benthic alga, has been shown to be proportional to the size of the stones to which it is attached, but in slower water, thallus size is independent of stone size. The bulk of this alga increases more rapidly than the area of its attachment, and the current limits the maximum size of the thallus, either tearing the thallus away from the stone or transporting both stone and thallus to a slower part of the stream (169).

Diatom species characteristic of different current rates are listed by Butcher (41) and Cholnoky (51). *Stigeoclonium tenue*, and probably other riffle algae as well, can be found growing over an extremely wide range of current velocities, including velocity of zero, provided, in the latter case, that the still water surrounding the alga is only a few centimeters distant from water in active movement (20).

There is general agreement that rapid streams are likely to carry a greatly reduced potamoplankton (1, 4, 53, 79), and Schröder (205) formulated the rule that the gradient of a stream is inversely proportional to the density of its plankton. It is well known that floods are destructive to stream invertebrates (235), and Galtsoff (85) and Fjerdingstad (74) have cited examples of the depletion of plankton by rapids or a cataract. It may be concluded, there-

fore, that rapid current represents a mechanical danger for phytoplankton organisms, but that attached or other benthic algae are in some way benefited by moderate current.

It is worthy of note at this point that the vegetation of rapids in the temperate zone is almost limited to the lower cryptogams; the aquatic angiosperms have thus far been largely unsuccessful in establishing themselves there.

WATER LEVEL

Except for algae which are left high and dry, fluctuating water level seems to be important principally for the changes which it causes in current velocity and direction. Chemical and biological changes accompanying changes in water level are discussed below.

At times of low water, the volume of flow and current rate decline, nutrient depletion is increased, and nutrient replacement is decreased. With lowered water level, the mouths of rivers at sea level may become brackish, and smaller streams may stop flowing entirely. Under these latter conditions, a stream may become converted into a series of pools, and either death or dormancy is imposed on the riffle biota.

There is evidence, however, that production of phytoplankton is increased in periods of low water (64, 116, 204) and that euplankton organisms become more abundant at this time (6). Both photosynthesis and decomposition exert their greatest effect upon the environment under low-water conditions (154), and it is probable that these processes are themselves profoundly influenced by approaching stagnation. Slow rivers, such as the Mayenne (France, 9), may flow only during the rainy season. At other times their plankton, like that of the Thouet (France), another slow stream, may be expected to show similarities to pond plankton (54). Fresh-water algae seem to fruit more abundantly at periods of high water than at low water (227), but the factors involved are certainly much more complex than water level or current rate.

The usual flood period varies widely, even for northern hemisphere streams, and minor floods may apparently occur at any time during the year when upstream drainage is of sufficient volume to overflow the banks. At such times the river rises, its surface and average speeds are greatly increased, local currents on riffles change their orientation, and attached algae and other or-

ganisms are torn away from their substrate (124). Numerous rocks are transported short distances downstream, and smaller mineral particles are carried in great abundance; turbidity increases greatly, and the chemistry of the water undergoes marked changes. Small stones, along with dead branches and other upstream debris, become molar agents which erode the stream bottom and are eventually deposited on banks or shallows. Silt is likewise deposited, beyond shoals, in partially impounded areas, or in deeper water where current is slight. Mountain streams are raging torrents in a rainy season, and may be virtually dry the remainder of the year (151).

It has long been recognized that flood waters bring about great changes in plankton (55, 116, 160, 165). In temperate streams, usually a sharp decline in plankton occurs with rising water level, as drainage waters dilute the stream proper. When spring flood waters recede, however, a major plankton pulse frequently follows hard upon such recession. This was apparently first observed by Kofoid (116) in the slow-moving Illinois River, but has since been verified in other streams (14, 149, 187, 188, 198). There are many recorded examples of a delay in the production of this plankton pulse, however, and it is possible that it has no direct relationship with the preceding flood period. Kofoid concluded that enhanced phytoplankton production might be expected either with stability in water level over a period of time or with falling water level (116).

DEPTH

The relation of depth to the algae of rivers has received relatively little attention, and few detailed cases of zonation are on record. It is probable that nearly all streams which maintain a given water level for several weeks exhibit some zonation of the attached algae. The author (unpublished) has seen zonation involving two or three species many times in southern Michigan. The best place to observe such zonation is on the sides of large boulders which break the surface of the water. An unusually clear example of the zonation of nymphs and larvae of aquatic insects living on rocks in streams has been recorded (152), and it is probable that many algal societies exhibit similar patterns of distribution. The sides of river steamers plying the Volga show a

rather clear zonation, with an upper partly emergent layer (20–100 cm. wide) dominated by *Pleurocapsa fluviatilis*, next a submerged band 30–35 cm. wide of *Cladophora* and *Stigeoclonium*, and, lowermost, a third band, 50–60 cm. wide, composed of diatoms (*Cymbella*, *Gomphonema*, etc.) (65). Scheele has recorded diatom zonation in drains (Schleusenwände) in Germany, the most outstanding difference with increasing depth being a decrease in numbers of *Nitzschia palea*. *N. frustulum* was found most commonly in a transition zone intermediate in depth and in available light (200).

In general, depth of rivers is not great, and it is probable that algal growth in surface streams is not usually limited because of reduced light. However, in extremely turbid rivers, such as the Missouri and the lower Mississippi (71), light is reduced so rapidly with increasing depth that the latter must become a sharply limiting factor for small benthic and even for planktonic algae. In clear streams it is possible for algae to grow at considerable depths, as in the Seerhein, a part of the Rhine which connects the two parts of Bodensee (134). Here numerous algae, including *Hildenbrandia*, *Lithoderma* and *Cladophora*, have been recorded growing at depths of seven to 25 meters.

TEMPERATURE

One of the characteristics of natural waters is the relative uniformity of temperature which prevails within them from day to day. Land habitats may be exposed to considerable seasonal as well as diurnal fluctuations; for any given period, and with few exceptions, the neighboring bodies of fresh water will show slower temperature change, and lower maximum and higher minimum temperatures. Although temperature conditions in streams are essentially different from those of lakes, this moderation of temperature is characteristic of both.

Temperature change in streams is much less rapid in the region downstream from impoundments. In such situations, and especially in seasons of great thermal change, the pond or impoundment acts as a thermal stabilizer which eliminates great diurnal fluctuations in water temperature in the stream. It is possible that certain floristic differences between different parts of the course of a stream are due to such differences in thermal phenomena (20).

In streams of temperate and cold regions, the cold season may be characterized by an ice cover on the stream. In high latitudes this ice cover is of considerable importance; in the Piasina (U.S.S.R.), for example, it lasts for nine months of the year (90). Total plant growth reaches its minimum under the ice cover (232), but little or no quantitative work on this question has been done.

The warm season is the period of maximum growth for most algae; but, although this growth is often dependent on warmer temperatures, there is no evidence that the blooms and rapid seasonal development of various algae occur as a direct result of temperature rise, for these pulses may apparently come at any time or times during the spring, summer or fall, and be of relatively brief duration. Butcher (39) calls attention to a spring pulse of diatoms in the Wharfe (England) which clearly precedes the period of high temperatures. Most brook algae are better adapted to low than to high temperatures. *Ulothrix zonata* grows best below 15° C. and can produce zoospores in ice water at 0–1° (158).

In tropical waters there may be little seasonal change in temperature, and it may be concluded *prima facie* that any seasonal change in the vegetation of such streams is not due to temperature change (160).

In a comparative study of small upland brooks (Sauerländische Gebirgsbäche, Germany) with a lowland river, the Ruhr, Budde (35, 36) concluded that temperature is a limiting factor in the distribution of *Diatoma hiemale* which was common in the smaller and cooler waters of the upland streams but could not withstand the greater temperature fluctuation of the Ruhr. Several diatoms grew best at temperatures between 3° and 10° C., and disappeared from the Ruhr in July and August, apparently being unable to survive above 19 degrees. Maximum development of *Melosira granulata* has been recorded at periods of both high and low temperature (165), and Pearsall has concluded that the real causes of diatom periodicity are probably factors operative during cold weather but which may have no causal connection with temperature (165). In temperate habitats the period of maximum change in temperature comes in spring and in fall. Since there also are profound changes taking place at this time in the available light, in the chemistry of the water and in the biota, it is often impossible, on the basis of field observations, to draw any reliable conclusions

as to the precise relation between temperature and any specific photosynthetic organism or group of organisms.

Most streams are of such slight depth that no real thermal stratification occurs in moving water, not even in so large a stream as the Volga (11). When two water masses exhibiting essential physical or chemical differences occupy an impoundment, however, there is frequently little mixing between the two, with the result that a warm layer may be found above a colder layer. Hydroelectric impoundments are cited as examples by Ellis (71) who states that they may be composed of a "warm, muddy river" flowing over a cold clear lake which exhibits no water movement in the hypolimnion and little in the thermocline. Another example of stratification is given by Fridman (77), whose work on the Kama (U.S.S.R.) demonstrated the presence of relatively warm industrial sewage spreading out over the surface of the water without much affecting the deeper water. For temperate streams generally, it may be concluded that differences in vegetation within a small area are not usually caused by temperature differences. For vegetational changes from source to mouth, however, as well as for seasonal changes, temperature remains one of the more plausible causative agents.

LIGHT

It is clear that algal photosynthesis and hence algal growth are as dependent on light as are the same processes in higher green plants. The presence of a unidirectional current in the habitat of river algae, and the linear nature of the basin, present problems in relation to light which are, however, somewhat peculiar. The author's work on streams in southern Michigan indicated that the amount of light reaching algae growing near the surface does not appear to differ greatly in amount from that reaching low herbs which grow on adjacent banks. An alga growing in an unshaded position must therefore be able to withstand full sunlight almost unreduced in amount, and its photosynthetic system in return enjoys the advantages of copious radiant energy. However, in all except streams flowing through a barren landscape, there are few positions on the stream bottom which remain constantly in the sun, and probably very few also which remain constantly shaded. Peculiarities of the stream's course, the character of the bottom,

and particularly the ever-present bank vegetation, militate against such constancy of incident light. Hence the amount of radiant energy reaching a given river alga can almost never, even on cloudless days, be expected to follow the curve for total light reaching a point on the earth's surface, but instead, for a given depth must range between the curve for a sunny position and that for a shaded position. It is evident that bank vegetation thus reduces the incident light sharply in summer, and the author's data indicate that a similar effect obtains in winter. The leafless branches of overhanging trees appear to have virtually no effect in reducing diffuse light from a cloudless sky, however. Shaded riffles in winter owe this characteristic (shade) to a factor which at the latitude of Michigan is inoperative in summer, namely, the trunks and large branches of trees located 20 to 50 meters from the stream on its southern side. Such trees, provided the sun can clear them, may have no effect on river algae in summer, even though they are in full leaf, whereas in winter they sharply reduce the incident light reaching the stream (20).

The profound effects of deep shade on stream algae are evident in the meagre vegetation of streams passing through the mature beech-maple community of northeastern United States, whereas the same stream passing through a clearing is usually well populated with algae. Transeau (227) has observed that algae established in shaded portions of streams are able to grow but may never reproduce there. In the experiments of Reese (185), shading greatly reduced algal colonization on slides in the streams Rheidol and Melindwr (England). One would expect shade-tolerant forms like *Batrachospermum* spp. to yield quite different results. In clear water *Hildenbrandia*, which is an extreme shade-tolerant form, may be found only on the sides and undersides of rocks (142).

In Butcher's experiments (44) it was noted that the number of algae appearing in five days on submersed slides was nearly always greater when the amount of sunlight was greater; this suggests that fair weather at least induces more rapid growth of the algae. In reference to the optimum growth period of *Ulothrix zonata*, *Cladophora glomerata* and their epiphytes in the upper Rhine, Jaag states: "Die Sonne scheint diese Massenentwicklung hervorzurufen. Folgt darauf eine Reihe trüber Tage, dann ist die ge-

samte Vegetation bis auf wenige Reste verschwunden. . ." (107, p. 65). A similar correlation between disappearance of the *Cladophora* vegetation and leafing out of the overhanging trees was evident in the author's work on the Saline River (20).

TURBIDITY

Variation in total radiation with depth is probably of relatively minor importance in a small stream, but in a large river bearing a heavy silt load, turbidity can reduce light penetration to a point which curtails or completely prevents plant growth, including that of phytoplankton. Near base level and near the mouths of large streams, silt, clay, plankton and other materials in the water may combine to produce high turbidity levels. Under such conditions a decrease in phytoplankton is sometimes noted, apparently due to the reduction in light penetration caused in part by the plankton itself (69). In most parts of the lower Mississippi, light is reduced to one millionth its surface intensity at depths of only 200 to 400 mm. (71). In the lower Missouri River (U.S.A., 18) turbidity is commonly greater than 3000 ppm., and the factors which tend to produce turbid waters adversely affect almost every characteristic of the river in this region—a high water temperature of 82° F. has, for example, been recorded here.

Such sharp reduction is uncommon in smaller streams in the temperate zone, but relatively high turbidities (200–300 ppm.) occur in eroded watersheds after heavy rains and following the melting of large quantities of snow and ice in winter and spring (20, 180). This is usually dispersed in small streams after two or three days, partly by sedimentation and partly by flushing out of the turbid basin by fresh supplies of water. Below the points of entry of sewage effluents, an increase in turbidity can usually be noted; this disappears with distance downstream if the volume of sewage is not excessive in relation to the volume of water which dilutes it.

In terms of millionth intensity depth (the depth at which light is reduced to a millionth of its surface intensity), the results obtained by Ellis show a minimum turbidity or maximum m.i.d. of 53.9 m. for a mountain stream in Mexico, and a minimum m.i.d. of 84 mm. for the Missouri River (71).

The deposition of silt which follows a turbid period in streams

is of great importance for unicellular algae, e.g., *Closterium acerosum* and *Cymatopleura solea*, which live on silt banks and which may be quickly covered at such times by new and extensive silt layers. Unless they can move up to the surface of the sediment, they are likely to suffer widespread destruction. Little work has been done on this question, although data showing a similar lethal effect on bivalves of silting has been obtained (71). The larger filamentous algae, such as *Cladophora glomerata*, serve as traps for silt under these circumstances. The water within their tangled thallus is slowed and its burden of sediment is largely deposited, rendering the entire thallus heavy and screening its lower portions from the light. Soon the plant is semi-rigid with its load of silt, and under these conditions much of it is either killed off or torn away (author, unpublished).

CHEMICAL CONDITIONS

DISSOLVED GASES. The biological significance in streams of the dissolved atmospheric gases is similar in many respects to their significance in other waters, and the reader is referred to a text of limnology (197, 235). The behavior of these gases is in general similar in both lenitic and lotic habitats, although the influence of the current is such that oxygen is seldom depleted in streams. Even in highly polluted situations, dissolved oxygen may reach supersaturation (74). The course of dissolved oxygen on a stream profile is dependent on many diverse factors. Streams issuing from springs tend to be low in dissolved oxygen (211, 234), but usually the upper course of streams in temperate regions is well oxygenated (172). The entry of an important sewage outfall, other things being equal, will tend to depress the dissolved oxygen. Empoundment of the stream or retardation of its flow, as in the lower course of most streams where deposition and decomposition of bottom sediments occurs, may likewise serve to depress the dissolved oxygen (108), although data are conflicting. An abundant vegetation, either benthic or of phytoplankton, may completely suppress this tendency toward depressed oxygen values. The work of Powers (172) shows that many rivers which drain lakes have a higher dissolved oxygen content than the waters of rivers not fed by lakes. In some streams the profile curve for carbon dioxide resembles the curve for dissolved oxygen in reverse, with an in-

crease in one occurring in response to factors which tend to depress the other (108). Thus the presence of a cataract tends to increase the dissolved oxygen sharply, but likewise to remove significant amounts of carbon dioxide from the water.

Photosynthesis during the day tends to reduce the free carbon dioxide and to increase the dissolved oxygen, whereas respiration, occurring at all times, has an opposite effect. This results in a diurnal pulse in these gases (16, 20, 31, 48, 63, 95), with oxygen somewhat depressed during the night hours and carbon dioxide during the day. Seasonal variations in dissolved oxygen have also been demonstrated, the values being somewhat higher in winter than in summer (75, 108, cf. however 181), but the evidence for carbon dioxide is not so clear. Neel describes a limestone stream in which free carbon dioxide is present only during a brief period in early autumn (154). Complete oxygen exhaustion may occur at night in highly productive lagoons (235), and the same phenomenon probably occurs in silted backwater areas connected with a stream only by a shallow and narrow mouth. A similar condition is probably present in streams which come to a stop in dry periods of summer and fall, as well as in rivers which flow only during a rainy season.

pH. Unless they receive the acid drainage from mines or other mineral deposits, streams apparently do not attain highly acid conditions similar to those of bogs and moor waters (235). In streams receiving mine seepage, acidities of pH 1.8–3.0 are common. Lackey reports *Chlamydomonas* spp., *Navicula* spp., *Desmidiium* sp. and *Euglena mutabilis* at pH 1.8 (125, 126). *Ulothrix zonata*, *Stigeoclonium* sp. and *Mougeotia* sp. were found sparingly at pH 4.0 or lower (125), but this work emphasizes the general scarcity of plant life characteristic of these habitats. The tropical streams studied by Sioli (211) mostly exhibited relatively low pH. There is probably a tendency in many small streams draining temperate moorland areas to be somewhat acid in their headwaters, and to approach neutrality downstream in proportion to the distance from headwaters areas. A case in point is the Ry Colas (Belgium, 61).

The neutral or slightly alkaline conditions which are characteristic of most temperate streams appear to be prerequisite for the

majority of algal species inhabiting flowing water. Foged, quoting Hustedt (101) and Iversen, has pointed out that alkaline lakes may have four times as many species of plants as acid ones (75); an examination of Lackey's work aforementioned suggests that the same is probably true for stream habitats. The diatoms of several European streams have been classified as to their presence in or absence from streams of different reaction. Few species are "acidophilous", the majority being listed as "alkaliphilous" or "alkalibiontic" (75, 199).

Probably most streams which possess some limestone in solution are well buffered and exhibit little variation in pH beyond the range of 6.8–8.8. Brujewicz (31) and Hanoaka (94) have recorded a diurnal variation in pH, with somewhat lower values being obtained at night than during the day (cf. 67, however). In a small creek the rapids tended to be somewhat more alkaline than pools, probably due to the removal of free carbon dioxide from the former (62). Such removal of carbon dioxide is also effected by photosynthesis and may result in an annual variation in H-ion concentration, as in the Thames (188). Here the pH attained a value of 8.5 in the spring, at the time of the phytoplankton maximum, and was relatively low in summer, fall and winter. Unusually high pH values may be characteristic of the water in the neighborhood of beds of benthic algae or other aquatic plants during daylight hours. Usually, moderate flow is sufficient to mix the water and prevent excessive alkalinities from being attained, but it may be supposed that conditions of summer stagnation will stop the mixing process and make life impossible for certain acidophilous species.

CALCIUM. The presence of calcium in fresh waters, and its relation to aquatic organisms, is the subject of an extensive literature, including important monographs by Prát (173) and Pia (168). Calcium behaves in streams much as in other fresh waters. A large number of algae and other organisms precipitate the monocarbonate in essentially the same way, but it is not always easy to determine which algae are lime-formers and which are lime-perforators (240). Frequently, as in marl lakes, the rocks on the stream bed become covered with a coating or a crust of marl which is secreted as crystals between adjacent algal filaments or cells, or, in some cases (e.g., *Cladophora*) as a shell or sheath around the

algal filament. If the marl is present as individual crystals, it undoubtedly experiences constant erosion by the current, which may explain the extremely slow growth of some of these algal crusts. If the algal filaments grow in compact tufts, as do *Phormidium incrustatum* and species of *Schizothrix* and *Amphithrix*, the crystals of lime tend to accumulate at the base of the filaments, thus rendering the interior portion of the crust hard-packed and brittle, while the outer portion remains more cushion-like in texture.

In hard-water regions of the world, the principal algae of streams are lithophilic and calcified in this way (20, 114, 134). The absence or near-absence of calcium from the water may result in a peculiar flora which includes many Myxophyceae (46). Waters rich in lime, other things being equal, tend to be rich in algae. Reinhard (187) cites the Minnesota River (U.S.A.) as an example—he estimated that this stream, which contains abundant carbonates, produced an average volume of plankton six times that of the nearby St. Croix River which is poor in carbonates and contains humic acids. In distinguishing eutrophic from oligotrophic streams in Britain, Butcher (46) stated that the principal factor bringing about eutrophication might be one or several of the dissolved mineral salts; it was concluded that calcium, however, is not the factor which determines the presence of the principal species.

PHOSPHORUS. Unlike the sea and fresh-water lakes, where surface nutrients are frequently depleted early in the season of favorable temperature, rivers do not generally exhibit marked depletion, although much fluctuation is characteristic (166). Under special conditions in waters where phosphates are almost insoluble, they might represent a limiting factor. A distinct increase in dissolved inorganic phosphates seems to be characteristic of summer months (16, 20), although the phosphates do not necessarily diminish to limiting levels in other months. If substantial amounts of agricultural drainage or sewage empty into a stream, an increase in phosphorus is expected at and below this point for a considerable distance, and the favorable effect on algal growth is frequently striking in this region.

NITROGEN. Since nitrates are carried into streams by runoff water, they tend to be more abundant at times of heavy rains or melting of snow, and hence are at a high level during the winter and spring months when streams are high and plant growth is

greatly reduced (20, 39, 116, 165). The same tendency is seen in other streams for other nitrogen compounds, but it is not possible to state that for streams, generally, specific seasons of the year are characterized by maximal or minimal quantities of any one stage of the nitrogen cycle.

The progressive destruction and oxidation of nitrogenous compounds in streams is the subject of an extensive literature (summaries or discussions in 43, 46, 70, 74, 99, 121). The profound fertilizing effect of these substances is evident in most polluted streams. Depending largely on the respective volumes of flow of the stream and of the outfall, and on the degree to which the sewage has been decomposed before being delivered to the stream, a changing flora is found downstream from the outfall, with various algae becoming dominant as successively distant reaches of the river become, upon bacterial action, rich in amino acids, then in ammonium compounds, and finally in nitrites and nitrates. An abundant European literature exists on the species of microphytes and small invertebrate animals which may serve as "indicators" of the respective "zones"—the latter being based largely on the degree of reduction and oxidation of these nitrogen compounds (*vide* Kolkwitz and Marsson, 122; also 36, 74, 99, 137, 156). As research continues on this subject it has become clear that many organisms are useful in determining the degree of pollution and the limits of the various zones in the Kolkwitz-Marsson system (74, 163), but that the "indicator" organisms themselves are not unerring indicators: the algae are much more trustworthy if growing on the bottom (72, 156) and if they are present in large numbers (36, 74, 237). Lists or discussions of the species characteristic of the different zones of a polluted stream may be found in 20, 36, 45, 72, 74, 99, 115, 122, 137 and 237.

The position of the "zones" of a polluted stream, and hence their flora, are not necessarily permanent but may be expected to advance in a downstream direction at any time when augmented pollution increases the increment of decomposing solids. There is some evidence that the same phenomenon occurs in winter when cold weather retards bacterial action to such an extent that the respective algae characteristic of nitrite- or nitrate-rich waters thrive only at specific points well downstream from their summer habitats (20, 47, 86, 167).

From the botanical standpoint, the most significant effect of

organic pollution in a stream is usually one of fertilization and enrichment. The total number of species is generally reduced, but those which grow are likely to grow massively, with a corresponding increase in total production. The density of plankton or benthic algae may be reduced temporarily by large accessions of sewage (26, 27, 43, 209), and the deleterious effect is most apparent if anaerobic conditions prevail (128). If the stream receives so much organic matter that the normal biotic community is largely or completely destroyed, the algae are likely to be entirely exterminated for a minor or major portion of the stream's course (46). At the downstream end of this zone of putrefaction, *Nitzschia palea*, *Gomphonema parvulum*, *Phormidium uncinatum* or *P. autumnale*, *Ulothrix zonata*, *Stigeoclonium tenue* and various species of *Oscillatoria* may make their appearance as benthic algae. Perhaps the most conspicuous and resistant forms are *N. palea* and *G. parvulum*, which frequently become dominant somewhat below the zone of putrefaction (46). Usually the algae as a group exhibit enhanced growth immediately, or a short distance downstream from the outfall (20, 135). The effect of the algal growth is a generally favorable one for the region where the algae are growing and providing abundant oxygen. But downstream areas may be affected deleteriously because of the greatly increased amounts of organic matter produced by algal photosynthesis and eventually decomposed, partly *in situ*, but mostly, in all probability, a short distance downstream after temporary transport of moribund thalli by the current.

The relation of seasonal nutrient variation to algal growth is discussed below under "Periodicity".

SALINITY. Those streams, both large and small, which debouch into sea water exhibit at their mouths a region of varying salinity which fluctuates in length and in depth with the tides and to a certain extent with the seasons. Under these conditions the flora of the stream changes, many species limited to fresh water being killed off, and new forms, which are characteristic of brackish conditions or which exhibit enhanced growth in the presence of new nutrients brought in by the tide, making their appearance (8, 29, 93, 134, 157, 175, 220). A few "fresh-water" algae, such as *Cladophora glomerata*, may grow very successfully in estuarial

waters in apparent response to the increased concentrations of limiting salts or other nutrients (93). Wood and Straughan (238) observed reduction in size, as well as sexual retardation, in *Le-manca fucina* growing in a stream where it was exposed to brackish water twice daily.

The effect of tides on polluted streams which enter the sea is frequently a favorable one, since the diurnal ebb and flow is sufficient to mix sewage and other pollutants with large amounts of water (175, 232). The extensive tidal flats which are present in many estuaries permit rapid decomposition, and a dense vegetation of angiosperms and algae develops there.

The tendency for acids and alkalis in industrial wastes to neutralize each other results in an increase in salinity downstream from important outfalls (118). Under these conditions, halophytic and salt-resistant diatoms may grow and reproduce.

OTHER SOLIDS. We may suppose, *a priori*, that the mineral nutrition of river algae depends upon the same essential elements that are necessary for other green plants. Few if any nutritional studies have been carried out on strict rheophytes, but the role of some of the chemical pollutants has received considerable observation and comment, and there are indications that one or another element is necessary, stimulating or toxic for certain river algae (36, 112, 157, 192, 207, 229 for iron; 192, 207 for copper; 110, 184, 192 for zinc; 20, 96 for chromium; 207 for boron and phenol). Without studying these problems *in vitro*, it is possible to obtain highly suggestive indications of the significance of certain elements because of the chemically peculiar nature of outfalls or tributaries which may enter a stream. In some cases there is little physico-chemical difference between a stream and such a tributary, and where a single factor varies significantly between the two, the conditions for a valid ecological experiment are met. Sometimes there is a marked difference in the fauna or the flora of a stream above and below the entrance of such a tributary, a difference which is highly suggestive of the role played by the variable factor or factors which the tributary introduces. Frequently, too, there is little mixing of the two waters for some distance below the entry of a tributary or an outfall, and obvious differences between the biota of the left and right banks of a stream betray the character of the

respective streams of water. Probably the best field conditions for observing specific effects of industrial effluents are met by small streams on which are located isolated industries (228). The latter sometimes deliver wastes which are relatively simple and relatively constant in composition as compared with streams in general.

Specific poisons entering the stream in significant amounts may result in complete suppression, in an extensive area downstream from the outfall, of species which are abundant or even dominant above the outfall. In the author's work on the polluted Saline River (Michigan), *Cladophora glomerata* behaved in this way, returning to the river flora only after several miles of meanders had permitted the dilution, precipitation, and adsorption of poisonous ions to which *Cladophora* appears to be very sensitive (20).

PRODUCTIVITY AND EUTROPHICATION

Because of the absence of thermal stratification from streams and of the accompanying chemical phenomena, as in lakes, the concept of eutrophy undergoes considerable distortion when applied to stream conditions. Many authors treating river ecology have retained the terms "eutrophy" and "oligotrophy", apparently employing them as approximately equivalent to "high productivity" and "low productivity", respectively. Few readily accessible streams now exist which have not been influenced by man, and the organic pollution, which is man's characteristic legacy to the streams around him, thus results in increased eutrophy, unless, as sometimes happens, other deleterious substances released to the stream are sufficiently concentrated and sufficiently lethal to inhibit growth of higher organisms generally. The fertilizing effect of organic pollution may be most conspicuous after several years and at a distance of some kilometers below the source of pollution (25, 234). Immediate effects may be detrimental to fish as to phytoplankton (26), but beyond a certain point, productivity shows a marked upswing (cf. nitrogen above).

Schmassmann has correlated the saprobic system with the trophic scale by a study of diurnal changes in dissolved oxygen, which he regards as an excellent device for estimating the course and intensity of metabolic events in streams. As a result of delivery to the stream of organic wastes, an allochthonous zone may replace a region of organic production based on autochthonous ac-

tivities. In oligotrophic waters both oxygen consumption and oxygen production by the vegetation are relatively small. The lowest concentration of dissolved oxygen in such streams is to be expected in the daytime hours because of diurnal temperature change in air and water, but variation in dissolved oxygen is essentially minimal. In a eutrophic (or β -mesosaprobic) stream, catabolic and photosynthetic activities are both greater. The dissolved oxygen is similarly influenced by solar radiation, but due to increased photosynthesis may reach much higher concentrations at midday than at night; a slight oxygen deficit is to be expected during nocturnal hours because of the respiration of relatively dense populations. In a truly allotrophic or polysaprobic situation there is no influence of photosynthesis on the dissolved oxygen of the stream. A periodicity in the latter is, however, to be expected, with higher values being recorded during the night because of the usual variation from night to day in the amounts of organic wastes delivered to the stream from human communities (203).

Most of the usual criteria of productivity in bodies of standing water, such as depth, biota and the organic content of the water and of bottom deposits, are applicable, with certain modifications, in streams. The great ecological variability within short distances in streams renders more difficult, however, the sampling procedures necessary to precise measurement of any of these factors. Workers interested in such problems regarding river algae, particularly benthic forms, will find that methods comparable in precision to those now applied to a study of fresh water and marine plankton can be worked out readily enough, but it is likely that such methods will be distinctly more time-consuming and will demand even greater care and patience on the part of the operator than do standard plankton methods of the present time.

Impoundments, abandoned meanders, and backwater areas along the course of the stream have been mentioned by various workers as breeding grounds for the plankton of the stream, and the claim is made (183) that productivity is dependent upon the presence of such biotic reservoirs. At least it seems likely that a stream which has few or no bodies of standing water in its basin is constantly threatened with thorough scouring and rinsing whenever the water rises, and, possessing no adequate reservoir in which unattached organisms may remain to repopulate the water after sub-

sidence of the flood, the stream loses most of its plankton (119). Productivity must be severely curtailed under these conditions. On the other hand, a stream which is poor in nutrient substances and in productivity can probably be changed within the space of a few hundred meters to one of relatively high productivity by the interpolation of a eutrophic lake or impoundment (20, 150, 211). Left to itself, it would appear that a stream through its own maturation processes should over a period of centuries increase in eutrophy in its lower course (cf. 63).

Productivity is certainly dependent upon the speed of the current, the size of the stream, and the nature of the bottom, but interest here has usually been centered on planktonic rather than benthic forms. The work of Lastochkin (131) indicates that biomass is greater in pool regions than in riffles (cf. 92, 152, however). The biomass may be greatly increased in a polluted stream by hard pieces of industrial refuse on the bottom (77). Some streams, e.g., the Mississippi (85), exhibit striking variations in productivity within relatively short distances. For discussions of insect and fish productivity see Lastochkin (131) and Vivier (230).

Butcher, employing the submerged-slide method which he worked out, estimated that in eutrophic waters the average number of benthic algae colonizing such slides lies between 2000 and 10,000 per square millimeter of surface area (44). In the Tees River (England), investigated by him and his co-workers, a community dominated by *Chaetopeltis* and *Achnanthes* was characteristic of oligotrophic portions, whereas the lower eutrophic reaches were dominated by a *Cocconeis-Ulvella-Chamaesiphon* community. He considers the latter community to represent a climax association which increases in importance with the progressive eutrophication of the stream (44). The *Cocconeis-Chamaesiphon* community has also been observed to succeed (in a downstream direction) the algae of the upstream poly- and mesosaprobic zones. It is hence regarded as characteristic of an oligosaprobic but eutrophic situation (45).

Israelson (103) divides Scandinavian streams into two types: (a) a *Vaucheria* type (eutrophic) which is characterized by *Vaucheria* spp., *Cladophora glomerata*, *Hildenbrandia*, *Batrachospermum*

boryanum, *Chaetophora incrassata*, etc.; and (b) a *Zygnema* type (oligotrophic), characterized by *Spirogyra* and *Euglena* spp., *Hydrocoleus*, *Mougeotiopsis calospora*, *Schizochlamys* sp., etc. The latter type includes all the largest Scandinavian rivers. While it is too early to draw conclusions about streams of other continents, none of the precise "types" described by Israelson or by Butcher has been specifically identified in North America.

As concerns plankton organisms, various European workers have regarded *Tabellaria fenestrata* (233) and *Stephanodiscus hantzschii* (74, 122, 178) as characteristic of eutrophic streams. Probably to a considerable extent the species-lists which have been published for the β -mesosaprobic level of the Kolkwitz-Marsson system (74, 122, 178) are valid for eutrophic streams generally. Problems of productivity concerning both planktonic and benthic forms are discussed further in the following sections.

DISTRIBUTION IN TIME

REPRODUCTION

Vegetative reproduction is probably the commonest, and for many species of river algae the only method of reproduction. The types of spores and other reproductive bodies formed by fresh-water algae are described in various manuals of algal morphology (82, 158, 212). In addition to the usual holdfast (*Ulothrix*, *Oedogonium*), benthic species commonly exhibit a basal portion which can apparently persist from year to year (*Cladophora*, *Stigeoclonium*), giving rise to new branches to replace the earlier branches which have matured and broken off. In some species probably the only cells remaining in the unfavorable period are those which occupy unusually well-protected positions in rock fissures, or those which are partly buried in superficial sediments. From these positions they can repopulate the stream during a subsequent favorable period. Some species pass the unfavorable period as thick-walled spores, but many others appear to be as dependent upon sheaths or a "condensed" protoplast for winter protection as they are upon resting spores (217). Relatively few observations of the winter growth of river algae have been made. Brunnthaler recorded small benthic colonies of *Clathrocystis aeruginosa* during the winter in an abandoned meander of the Danube. Later, in warm weather,

he observed it reproducing and entering the plankton in quantity, becoming one of the dominant plankton algae (33).

Many river algae produce zoospores or zoogametes, and, while it would seem that the speed attained by stream waters would render such fragile bodies highly inefficient, the sudden and widespread appearance of thousands of young plants on the rock floor of rapids during the reproductive season, and even on fresh objects placed in the stream, shows the fallacy of this assumption. Presumably water movement is essentially nil in protected places on the floor of rapids or in minute crevasses in the rock, and the effect of current is to conduct favored individuals toward such a position and then to drive them into it. A positive rheotropism would be favorable to survival immediately upon release of asexual spores from a filament, and a negative response to current a short time later would be called for, but no work appears to have been done on this problem. It has been shown that the colonizing reproductive bodies of certain algal epiphytes have preference for small depressions such as the grooves between epidermal cell boundaries of submerged leaves (89). For summaries of work on the relation of temperature and light to reproduction, see Oltmanns (158) and Fritsch (82).

Many of the morphological problems connected with sexual reproduction of river algae have been worked out in standing water in the laboratory. Of those species which do not grow well under these conditions, much remains to be learned. Sexual reproduction and dissemination of strictly benthic forms are largely dependent upon currents (as are, indeed, the equivalent processes in limnetic algae), and in stream-inhabiting forms like *Lemanea* or *Batrachospermum*, which lack motile stages, this dependence is virtually complete. The widespread occurrence of centric diatoms in lakes and the sea bears testimony to the effectiveness of currents of all kinds as agents of mixing and dispersal.

Vaucheria species appear to fruit more frequently in standing water than in a current (49, 158, 212), and the same is probably true of *Spirogyra*, at least for certain species (103). In a stream community of *Spirogyra* observed by the writer, no sexual reproduction was found at any time during a period of nearly two years; the community, consisting of several species, waxed and waned and occasionally nearly disappeared throughout this time (20).

COLONIZATION AND SUCCESSION

It is clear that the term "colonization" is applicable to colonization of a new basin by pioneer organisms as well as to repeated colonization of upstream areas concurrent with the headward growth of the stream, by organisms already established in downstream or parallel waterways. Just how these processes are accomplished has not been demonstrated, but it seems probable that vertebrate and invertebrate, aquatic, amphibious and terrestrial animals are involved. Following the spring flood period in Russian streams, anadromous and semianadromous fish passing upstream were found to carry along parasites, seeds and eggs (131). In contrast to the ease of distribution in a downstream direction which all stream organisms and many riparian forms enjoy, reproduction and dispersal toward the headwaters is accomplished with great difficulty and may be supposed to occur for each species in numerous, but frequently small, steps, with much backsliding and loss of altitude.

Colonization by plankton forms has been discussed by Eddy (69) who regards the first occurrence of stable conditions in the stream in summer as the earliest opportunity for permanent colonization. He emphasizes the importance of the age of the water in plankton production and provides evidence that true plankton organisms are likely to appear in streams at a point six to ten days below the source if other conditions, particularly of temperature and turbidity, are favorable. Some small streams develop an extensive plankton population within a few miles of their headwaters, however, and the size of a stream does not seem to be any true indication of its plankton content (130).

The first colonists in a stream are probably diatoms and *Euglena*, whose resistant stages permit wide dispersal (68). In Spitzbergen the first units of a flora in streams of recent glacial origin are unicellular algae (219). The entire subject of plankton colonization is extremely difficult to approach, treating, as it does, microscopic forms which by definition are in motion from the start.

Colonization by benthic forms has been largely investigated by the methods of Butcher (41) which involve the submersion of blank microscope slides fastened in a photographic frame which is staked into the river bottom. At intervals a slide is removed from the frame and studied microscopically. A dry weight method for

total organic matter has also been developed. These methods permit quantitative appraisal of algal growth in its early stages. Apparently the method has not been adapted to long periods of observation, and no proof has been given that the algae colonize the slides in the same way that they colonize the river bottom. There is some evidence that numerical results from slide counts are not comparable to those from the river bottom, but that the species present are generally similar (184). From his work on the Hull (England), Butcher has concluded that colonization there reaches a maximum in May (43). Individual dominant species have periods of most rapid reproduction in various months from March through October (42), and the period of least colonization is in winter (43). In summer, colonization appears to be complete in about 20 days, but in cold months when growth is slower, 30 to 40 days are required (44). It might be supposed that vigorous current would impede algal colonization on so smooth a surface as a glass slide, but more algae are produced on the slides in regions of rapid flow than elsewhere (44).

In southern Michigan, colonization of rock surfaces by winter-dominant diatoms is very rapid, and macroscopically visible colonies can form in as little as ten days. The period within which *Gomphonema olivaceum* colonized bare rock surfaces extended from late November to early April, and colonization appeared to be possible at any time within this period (21). No evidence of succession was found prior to the establishment of this community, and the same may be said for a somewhat similar community of *Diatoma vulgare* characteristic of late fall—both these forms were at one and the same time colonists and seasonal dominants.

In the work of Butcher there is likewise little evidence of succession in the algal communities he has investigated. In the *Cocconeis-Chamaesiphon* community, *Chamaesiphon* arrives in the ensemble later than the other forms, but there is no true succession (44). Certain of these communities are regarded as representing a true climax, but their development is apparently accomplished with no steps separating invasion from climax conditions.

Allorge (5) has described a calcified association of algae (*Schizothrix*, *Calothrix*, *Gongrosira*) and mosses from flowing spring waters rich in lime. The community is part of a hydrosere and is followed by bog-like vegetation.

In 1929 Shelford and Eddy (210) posed a series of questions¹ regarding succession and designed to guide future research on lotic ecology. At present, few if any of these questions can be answered. The indications are that algal succession within a stream is less stereotyped and probably more intricate than certain well-known successions of plants on land.

CLIMAX CONDITIONS

Eddy has concluded that permanent fresh-water communities exist, reach maturity and show aspects comparable to terrestrial communities, and he points out that the maintenance of given climatic conditions necessary for the establishment of a "climatic" climax is not confined to land communities, but can also be found in permanent streams (69). The generation and the life-span of dominant algae are so much shorter than those of most dominant vascular plants that "permanent" climatic conditions can be achieved in a relatively shorter time, and more rapid succession is to be expected. For extremely short-lived microphytes, a single growing season in temperate regions may be sufficiently long to represent a "permanent" climate (23).

Panknin (161) has discussed the classification of seasonal communities which assume temporary dominance upon a given site, and concluded that such algae should not be regarded as constituting seasonal associations but rather as making up seasonal aspects of the entire association.

In streams it is the exception rather than the rule to find extensive areas inhabited by recognizable groups of algal species which maintain a definite order of dominance or inferiority with respect to each other throughout all the seasons, although this relationship is more commonly found if higher aquatic plants are considered (cf. 47, 193, 194). Extensive stands consisting of one or more species of dominant algae are relatively more common than among land communities. Often these stands are unialgal or

¹ These questions include, among others, the following: Do animals and plants gradually occupy stream bottoms denuded by flood or otherwise, until a fairly definite assemblage is attained? Is the presence of some organisms necessary for the invasion of an area by others? Do some organisms render conditions more suitable for other organisms than for themselves, thus producing succession? Do developing communities reach a stable stage if the conditions suggested above cease to take place?

nearly so, to the exclusion of other green plants below them. Many smaller species are epiphytes (or endophytes) on larger algae which support, and to a certain extent protect, them. The ephemeral nature of attached algae is furthermore one of the unique and significant features of stream ecology. With the detachment of a large thallus, it and its entire collection of epiphytes immediately start downstream. All these organisms with the foods and nutrients they contain are effectively lost to the local ecosom. In spite of such deep-seated differences between the communities of the stream and those of the land, the climax concept appears to be adaptable to many aquatic communities if care is exercised in the application of terms drawn from terrestrial ecology.

The *Phormidium-Schizothrix-Audouinella* epilithic community has already been described as an example of a climax in flowing water. Concerning plankton communities in streams, Eddy concludes, with particular reference to zooplankton, that certain organisms which are seasonal dominants in the early stages of plankton development in a stream, later become perennials when the conditions of life within the stream become more stable (69). Certain rivers appear to have particular phytoplankton organisms characteristic of their waters (134, 136), but this may be due at least in part to reproduction of these plankters within specific impoundments in the river basin. Whether or not rivers in general favor the production of one or more given communities of phytoplankton which can be found with regularity in streams over a large area seems at present undetermined. Further discussion of mature communities is given under the following Periodicity.

PERIODICITY

Twelvemonth records of the periodicity of fresh-water algae have been obtained from numerous streams, mostly in Europe and North America: Rio de la Plata (Argentina, 91); Danube (Austria, 32); Nile (Egypt, 1, 2); Hull (43, 44), Tees (41, 47), Thames (78, 188), Wharfe (39) (England); Garonne (59), Loire (56, 57), Mayenne (9), Midou (10), Thouet (56) and others (59) (France); Dortmund-Emskanal (177), Gauchach (234), Havel (19, 123), Lippe (37), Lenne (36), Main (111), Moehne (36), Rhine (133, 134), Ruhr (36), Spree (195), Werse (177), Weser (136), Wutach (234) and others (35, 178) (Germany);

Cooum (India, 106); Tjikoenir (159), Tjimoeloe (159) (Java); Biała Przemsza (214), Vistula (Wisły) (214, 242), Warthe (13, 97) (Poland); Limmat (138), Rhine (107) (Switzerland); Moscow (229), Oka (148), Volga (11, 12) (U.S.S.R.); Des Moines (215), Huron (50), Illinois (116, 117), Saline (20), San Joaquin (4) and others (30) (U.S.A.). Such is the diversity of the streams examined and of the results obtained, however, that few generalizations can be drawn.

PHYTOPLANKTON. Many streams exhibited considerable constancy, during the period and to the extent of the observations made, as regards the time of development of the greatest densities of their plankton or of their benthic vegetation (20, 57, 100, 116, 188), whereas other studies have pointed out sharp differences in the year-to-year developmental pattern (50, 148, 170). A mere year's work upon a single stream may prove inadequate in that it reveals conditions essentially unlike the preceding and following years. In nearly all streams investigated, the principal phytoplankton pulse, if there is one, is to be expected at some time during the warm season (28, 32, 53, 58, 90, 148, 187, 206, 208, 215), but individual plankters, e.g., *Crucigenia rectangularis*, *Pediastrum boryanum*, *Fragilaria capucina*, *Meridion circulare* and *Synedra ulna*, frequently exhibit population maxima in winter (10, 117, 197, 198, 214). Many streams are characterized by two separate periods of maximum plankton abundance (15, 100, 232). Some species of algae exhibit great variability in production, remaining uncommon in one year and becoming a dominant in the next, exhibiting a pulse at widely variable times throughout the year, or a single pulse in one year and a bimodal one in another. Certain diatoms tend to exhibit a pulse in spring and/or in autumn rather than in midsummer (118, 178, 232).

Occasionally a river may develop a "bloom", although this phenomenon is more frequently seen in ponds. Organisms which have been found responsible for such blooms include *Thalassiosira fluviatilis* (Weser, Germany, 34), *Synedra delicatissima* (Potomac, U.S.A., 60), *Microcystis flos-aquae* (Bug, U.S.S.R., 104), *Anabaena spiroides* (Mayenne, France, 9, 64), *Aphanizomenon flos-aquae* (Don, U.S.S.R., 52) and *Pandorina morum* (Cumberland, U.S.A., 129, and Kentucky, U.S.A., 228). Nearly all river blooms

appear to be due to the sudden reproduction of a single species, but an example is cited by Sørensen (Saxån, Sweden, 213) which involved several members of Volvocales. Lauterborn recorded water-blooms caused by a variety of diatoms in the Rhine estuaries (134).

The best correlations which have been obtained by plankton work and chemical analyses over a period of years point to a time relationship between abundant nutrients and abundant phytoplankton, the plankton pulse usually following the period of highest concentration of the nutrients, as nitrates and nitrites, in such a way that the decrease in nutrients precedes by a few days to a few weeks the maximum development of phytoplankton (100, 116, 185). In the work of Kofoid (116) and of Hupp (100) the plankton maximum occurred at a time when nitrates had passed a high level and were already decreasing. In the work of Reese (185) the development of various phytoplankton and benthic algae in Welsh streams followed some weeks after the decline in nutrient substances, while in the Thames (188) the phytoplankton pulse was approximately synchronous with high concentrations of oxidized nitrogen in the water. Hupp (100) believes that it is possible to predict high periods of phytoplankton development by observation of a previous decline in nitrate and nitrite nitrogen. In the River Hooghly (Bengal) the yield of phytoplankton was inversely correlated with turbidity, rainfall, and nitrate nitrogen (196).

The time sequence of seasonal changes in the production of such plankton pulses may be of less immediate influence, however, than the place sequence. Given sufficient warmth and a series of favorable days, the water chemistry in respective parts of various streams becomes the factor which determines the production of a dense plankton and of a dense benthic vegetation.

A diurnal plankton pulse has been observed in a polluted stream, apparently dependent upon and produced by midday sunlight which causes benthic forms to rise into the current and be carried downstream (22). Evidence that planktonic forms reproduce as they are carried downstream has been presented by various workers (12, 176, 187, 202, 230), but there remains the suspicion that much of the actual cell division occurs on the bottom and that the apparent increase in phytoplankton downstream is largely the result

of more extensive nutrient beds there, and of denser populations of benthic individuals, many of which rise every day into the plankton. The vegetative dissemination of *Spirogyra* and *Oscillatoria* communities was observed by the author on warm summer days in 1952 and '53. These communities were especially characteristic of quiet shoals or bays of the stream. Here the algae remained on the bottom in contact with nutrient-rich silt deposits, as masses of filaments easily visible from a distance. The surface water of such shoals and bays is usually in slow circular movement set up by the main current of the stream, which by-passes the shoal or the bay in a tangent to the circular current which it produces there. At times of rapid photosynthesis, individual masses of the algal filaments are detached and buoyed upwards by trapped oxygen bubbles. Once the algal mass has quit the floor of such a shoal, it is carried slowly along in the eddying surface water. After moving for some time in this circular manner, it may eventually be picked up by the tangential current of the main stream which removes it definitively from the shoal. As the algal mass travels downstream, it disseminates live filaments along the way. The progress of these filaments is arrested on obstructions or on new shoal areas or other sediments downstream, which in this way are themselves colonized. The elevation of algal masses by entrapped bubbles can be observed from about noon until about 2-3 P.M. on sunny days in summer, and the movement downstream of these floating masses can be observed throughout an entire afternoon (20).

BENTHOS. The principal method which has been employed to investigate the periodicity of benthic algae in streams is that of Butcher (40-44), which was described above. The same method has been taken over more or less exactly by various other workers (2, 87, 88, 105, 167, 184, 242). Butcher has also studied *Sphaerotilus* production by basing his data on dry weight per square inch (40). Foged utilized counts of diatom frustules on prepared slides (75). Hanoaka determined organisms growing on $5 \times 5 \times 5$ cm. cubes of cement which were placed in the water (95). Depth of color was employed by Bracher (24) in estimating the growth of *Euglena* on stream banks. Thurman and Kuehne (225) made counts of diatoms obtained from a 1×1 cm. cylinder of compacted algae. The author (20) employed sterilized rocks placed in a

stream for colonization studies, a dry-weight method for large algae, and a transect method involving a graduated rope stretched across the stream. A method for peeling off thin-layered epilithic algal communities has been developed by Margalef (145). Patrick, Hohn and Wallace have developed a special slide-holding apparatus ("Catherwood diatometer") which can be employed in sampling the diatom population of a stream (164).

The benthic algae of streams include both seasonal and perennial species. While a single alga may be dominant over relatively long reaches of the stream's course, it is more common to find a number of dominants with various parts of the stream having different dominant communities. In some streams the algal vegetation remains more or less the same throughout the year (167, 220), whereas in others there are marked seasonal aspects (20, 21, 30, 36, 41, 42, 111, 178, 234). Such seasonal aspects seem to be more marked in upland than in lowland streams (35, 36, cf. however 218).

One of the most striking phenomena in nature and possibly the one factor which has been most influential in attracting research workers into this field is that of the frequently abrupt changes which occur from month to month in the algal vegetation of streams. Visits to a small stream spaced at weekly intervals will often reveal the complete disappearance within a period of only six to ten days of an erstwhile conspicuous alga. Floristic changes from month to month may render the benthic vegetation completely distinctive in one season and visibly different from that of other seasons. Success, however, has not been generally attendant upon efforts to correlate such obvious biological results with environmental causes. It has likewise become clear with the appearance of successive papers describing the benthic vegetation of different European rivers, that streams which might be expected to have vegetations similar to each other in a given season, sometimes have quite different ones. As with plankton algae, the seasonal variation may be summarized broadly as maximum development in warm months, followed by minimum development in cold months, but many algae behave in quite different ways. To what degree these seasonal changes are due to differences in light or in length of day, or to temperature, or to chemical changes in the water, or to some other factor, has not been established. Among the few

conclusions that have been tentatively drawn are: *a*) that an extended period of low water with little change in hydrographic conditions is conducive to the full development of benthic organisms (36); *b*) that a period of several cloudy days can induce detachment and disappearance of certain algae (107); *c*) that an ice cover can bring about sharp changes in the vegetation; *d*) that periodicity of some forms depends on that of their epiphytes (80), while obviously that of epiphytes also depends on that of their algal substratum (107); and *f*) that leafing-out of bank vegetation has sharp repercussions in the stream (20).

One benthic species, *Cladophora glomerata*, whose ecology and periodicity have received considerable attention, has been chosen for consideration by itself.

Cladophora glomerata appears to be the most abundant filamentous alga in streams throughout the world. It is known to be highly sensitive to iron (20, 229) and relatively tolerant to high pH values (229). It is tolerant to relatively large amounts of sewage in the water (20, 167, 176, 233) and to weak salinity (93, 174). The length of its summer growth period may vary from a few days (42) to several months (35). Usually it is inconspicuous in winter, although Jürgensen has recorded its full development in February and March (111), Raabe in mid-October (178), and Jaag has observed it throughout the winter (107). It can apparently produce swarmers throughout the entire year (139). Freezing is not necessarily fatal to it (243). Sometimes it exhibits very rapid growth in spring, only to disappear very suddenly in late June or early July (20, 167). This may occasionally be caused by high waters, but it does exhibit generally poor growth in warmer streams in mid-summer (20, 225) and probably is sensitive to temperatures higher than around 25° C. The fact that individual plants can thrive at these temperatures while the remainder of the *Cladophora* vegetation has disappeared is, however, noteworthy (20). It reacts adversely to reduced light (20, 107) but has been kept in the dark for twelve weeks without entirely succumbing (243). After periods of turbidity the plants of *Cladophora* often become heavily loaded with silt and epiphytes, a factor which may be significant in the suppression of growth or in the mechanical detachment of the thallus. Satisfactory explanation of the comings and goings of this vegetation still awaits further study.

RELICTS

While long-term observation of the algal vegetation of streams has not been made, various workers have found in streams algae which may represent relicts persisting from a time when hydrographic conditions were essentially different (8), or species purportedly persisting from glacial times (178) or even from Cretaceous times (155). Tarnavschi (222) regards *Hildenbrandia rivularis* in Rumania as representing a relict persisting since the times of Tertiary seas; but the relict theory does not seem to explain its distribution in northern Europe (142).

DISTRIBUTION IN SPACE

LOCAL DISTRIBUTION

Most small streams consist of a series of alternating shallow areas ("shallows", "riffles") and deep areas ("pools"). The shallow areas naturally receive greater abrasion by the water and the molar agents it carries. The water flows faster here and in a thinner sheet, and significant chemical differences are to be expected between the shallows and pools, although little effort has been made to demonstrate them. Many algae are confined to shallow parts of headwaters streams, just as others are characteristic of the slower and deeper waters of pools or deeps. Peculiarities of the deeps and shallows as they alternate with each other on the stream profile determine the laws of distribution of the animal population as well (131). Succeeding riffles or shallows frequently carry the greater volume of water on alternating sides of the stream, so that erosion is greater first against the right bank and then against the left. This asymmetrical pattern results in asymmetric distribution of the benthos biocoenoses of the pools, with an accompanying break in their continuity at every riffle (131). *Ulothrix* spp., *Stigeoclonium tenue* and *Diatoma vulgare* are all characteristic of riffles and regularly drop out as massive components of the vegetation wherever pool conditions obtain. *Spirogyra* spp., *Euglena* spp. and other mostly unattached forms naturally collect where current is minimal. Within a riffle or shallows itself, certain areas are apparently much more favorable than others for the larger algae. Growth of *Diatoma vulgare* has been observed to be inhibited in the portions of the riffle downstream

from large rocks, where water movement is relatively slow. Growth of *Cladophora glomerata* is sometimes limited to the far downstream portion of a shallows area where water movement is slightly more rapid than elsewhere on the shallows (20).

The sides of a stream are ordinarily more shallow than the central portion, and the current is usually slower there. Other factors, particularly shade, may likewise be very different from those prevailing over the major portion of the stream bed. If one portion of the stream is to be regarded as more "typical" than another, the side areas are the least "typical" of all, and had best be left out of consideration when samplings to determine typical benthic stream vegetation are being made.

DISTRIBUTION WITHIN THE BASIN AS A WHOLE

Eddy (69) presented the view that the amount of plankton in river water is dependent upon the length of time required for the water to pass downstream from headwaters sources, or, as he regarded it, as the "age" of the water. Thus there is an initial increase in plankton with time and distance going downstream. Certain streams (e.g., the Illinois River (189) and the Rock River (76), both in U.S.A.) exhibit a headwaters area low in plankton and a middle region rich in plankton, followed by a consistent decline in plankton in the lower course. This decline is, however, not universal (cf. 85, 123, 202), and the phenomenon can not yet be correlated with a given length of course or degree of eutrophy. The subject is discussed by Welch (235, pp. 429-30). Conditions in a mature stream may be expected to approach those of late or middle-age ponds in the neighborhood of the stream whose waters have a similar chemical composition (68).

The changes in benthic algae over the course of a stream from source to mouth have been investigated by many workers (20, 35, 36, 38, 43, 61, 74, 98, 106, 107, 134, 138, 147, 149, 163, 184, 199, 207, 213, 230). One of the more exhaustive treatments of this nature is the work of Lauterborn (133, 134) on the Rhine vegetation. The great variability in size, profile, geology, degree of pollution, and other attributes of these streams does not admit of many comparisons of their respective floras, and little information of general application can be drawn from these studies until an extensive analysis of the data contained in them has been assembled. Probably

too, the make-up of the aquatic community is influenced to such an extent by chance that its permanent composition may be attained only after a very long period, centuries perhaps (221). Factors such as this operate to reduce somewhat the significance of the results of floristic surveys of aquatic habitats. An ambitious attempt to compare the flora of different streams has been made by Budde, who reviewed several published works on European and other rivers (36). Of the British streams studied by Butcher and his co-workers, the Itchen, Test, Bristol Avon, Hampshire Avon and Lark seem to be somewhat similar physico-chemically and to have many parallels in their algal vegetation (41). The work of Scheele (199) on diatoms of the Fulda (Germany) has shown that the tolerant ubiquitous species increase from source to mouth and that the species characteristic of springs show a corresponding decrease.

The agents capable of transporting organisms directly and specifically from one stream to another with no average altitude loss in the process must be few in number and relatively untrustworthy, although there are probably vertebrates capable of doing this (cf. 102). It would be of interest in this connection to know whether any plankton algae or their spores can survive passage through the digestive tract of animals which customarily drink at streams.

It seems probable that the evolution of distinctive river plankton forms has been retarded by the difficulties which plankton organisms experience in the dissemination of offspring to other basins. It is likely that the stream represents an unfavorable environment for plankters not entirely because of the mechanical and physical insecurity but also because of the inherent "dead end" nature of most streams, flowing, as they do, inexorably to salt water and death for all but those few organisms which can live and reproduce under brackish or marine conditions. A stream plankter with no ability to grow on the bottom is therefore in much the same position as, say, a trypanosome within the blood of a dying host. Possibilities of an assured future for its issue depend upon transfer to an entirely new host, a transfer effected in trypanosomes by leeches or by blood-sucking Arthropoda. Does the hypothetical obligate stream plankter possess any similar mechanism for transfer to a new lotic habitat? It seems likely that the greater survival value will lodge rather with the ability to grow facultatively either in quiet water or on the bottom.

BIBLIOGRAPHY

1. ABDIN, G. Physical and chemical investigations relating to algal growth in the River Nile, Cairo. *Bull. Inst. Egypte* **29**: 19-44. 1948.
2. ———. Seasonal distribution of phytoplankton and sessile algae in the River Nile, Cairo. *Bull. Inst. Egypte* **29**: 369-382. 1948.
3. ALGEUS, S. Untersuchungen über die Ernährungsphysiologie der Chlorophyceen mit besonderer Berücksichtigung von Indolylessigsäure, Ascorbinsäure, und Aneurin. *Bot. Not.* **1946**: 129-278. 1946.
4. ALLEN, W. E. A quantitative and statistical study of the plankton of the San Joaquin River. *Univ. Cal., Publ. Zool.* **22**: 1-292. Pl. 1-12. 1920.
5. ALLORGE, P. Les associations végétales du Vexin français. *Rev. Gén. Bot.* **33**: 481-543, 589-595 *et seqq.* 1921.
6. ———. Le plancton végétal de la Seine à Amfréville-sous-les-Monts (Eure). *Bull. Soc. Linn. Norm. VII.* **9**: 62-64. 1926.
7. ALTEN, H. VON. Hydrobiologische Studien über die Wirkung von Abwässern auf die Lebewelt unsere Gewässer. *Jahresber. Ver. Naturw. Braunschweig* **19**: 19-60. 1926.
8. ARNOLDI, V. M. Algues des rivières des steppes. *Jour. Soc. Bot. Russ.* **7**: 61-72. 1922.
9. BATARD, C. Note sur le phytoplankton de la Mayenne. *Bull. Mayenne-Sciences* **1931/2**: 1-14. 1932.
10. ———. Le phytoplankton de l'Adour et de ses affluents: la Douze et le Midou. *Soc. Linn. Bordeaux Proc.-Verb.* **84**: 32-56. 1932.
11. BEHNING, A. Das Leben der Wolga, zugleich eine Einführung in die Fluss-Biologie. *In*: A. Thienemann, *Die Binnengewässer*, Bd. 5. 162 pp., 2 pl. 1928.
12. ———. Über das Plankton der Wolga. *Verh. Int. Ver. Theoret. Ang. Lim.* **4**: 192-212. 1929.
13. BENNING, E. Die Schwebewelt der Warthe bei Landsberg. *Mikrokosmos* **15**: 182-187. 1922.
14. ———. Das Aprilhochwasser 1924 und die Planktonproduktivität der Warthe. *Arch. Hydrobiol.* **16**: 340-353. 1925.
15. ———. Das Plankton der Warthe in den Jahren 1920-24. *Arch. Hydrobiol.* **17**: 545-593. 1926.
16. BERG, K. Physiographical studies on the River Susaa. *Fol. Lim. Scand.* No. 1. 174 pp. 1943.
17. ———. Remarks on some Danish river studies. *Verh. Int. Ver. Theoret. Ang. Lim.* **10**: 76-79. 1949.
18. BERNER, L. M. Limnology of the lower Missouri River. *Ecology* **32**: 1-12. 1951.
19. BETHGE, H. Das Plankton der Havel bei Potsdam. *Arch. Hydrobiol.* **10**: 193-240. 1915.
20. BLUM, J. L. The ecology of algae growing in the Saline River, Michigan, with special reference to water pollution. *Doc. thesis, Univ. Mich.*, ix + 176 pp. 1953.
21. ———. Two winter diatom communities of Michigan streams. *Pap. Mich. Acad. Sci., Arts, Lett.* **39**: 3-7. (1953) 1954.
22. ———. Evidence for a diurnal pulse in stream phytoplankton. *Science* **119**: 732-734. 1954.
23. ———. The application of the climax concept to algal communities of streams. *Ecology* (in press).
24. BRACHER, ROSE. The ecology of the Avon banks at Bristol. *Jour. Ecol.* **17**: 35-81. 1929.
25. BRINLEY, F. J. The effect of the sewage from Nashville upon the plankton population of the Cumberland River. *Jour. Tenn. Acad. Sci.* **17**: 179-183. 1942.

26. ———. Relation of domestic sewage to stream productivity. *Ohio Jour. Sci.* **42**: 173-176. 1942.
27. ———. The effect of pollution upon the plankton population of the White River, Indiana. *Invest. Indiana Lakes and Streams* **2**: 137-143. 1942.
28. ——— and KATZIN, L. J. Distribution of stream plankton in the Ohio River system. *Amer. Midl. Nat.* **27**: 177-190. 1942.
29. BROCKMANN, C. Das Plankton im Brackwasser der Wesermündung. *Aus der Heimat-Für die Heimat. n.F.* **1**: 32-57. 1908.
30. BROWN, H. B. Algal periodicity in certain ponds and streams. *Bull. Torrey Bot. Club* **35**: 223-248. 1908.
31. BRUJEWICZ, J. Tägliche Schwankungen der hydrochemischen Faktoren im Flusswasser. *Verh. Int. Ver. Theoret. Ang. Lim.* **5**: 442-457. 1931.
32. BRUNNTHALER, J. Das Phytoplankton des Donaustromes bei Wien. *Verh. K.-K. Zool.-Bot. Ges. Wien* **50**: 308-311. 1900.
33. ———. Die Algen und Schizophyceen der Altwässer der Donau bei Wien. *Verh. K.-K. Zool.-Bot. Ges. Wien* **57**: 170-223. 1907.
34. BUDDE, E. Eine Wasserblüte der Weser. *Arch. Hydrobiol.* **18**: 316-318. 1927.
35. BUDDE, H. Die Algenflora des Sauerländischen Gebirgsbaches. *Arch. Hydrobiol.* **19**: 433-520. 1928.
36. ———. Die Algenflora der Ruhr. *Arch. Hydrobiol.* **21**: 559-648. pls. 33-36. 1930.
37. ———. Limnologische Untersuchungen niederrheinischer und westfälischer Gewässer. Die Algenflora der Lippe und ihrer Zuflüsse. *Arch. Hydrobiol.* **24**: 187-252. 1932.
38. ———. Die Algenflora der Eder. *Arch. Hydrobiol.* **28**: 240-253. 1935.
39. BUTCHER, R. W. The plankton of the River Wharfe. (Yorkshire) *Naturalist* **1924**: 175-180, 211-214. 1924.
40. ———. Biological changes brought about by sewage effluents in small streams. *Proc. Assoc. Managers Sewage Disposal Works (Kew)* **1928**: 168-185. 1928.
41. ———. An apparatus for studying the growth of epiphytic algae with special reference to the River Tees. *Trans. North. Naturalists' Union* **1**: 1-15. (1931) 1932.
42. ———. Studies in the ecology of rivers. II. The microflora of rivers with special reference to the algae on the river-bed. *Ann. Bot.* **46**: 813-861. Pts. 33, 34. 1932.
43. ———. Studies in the ecology of rivers. IV. Observations on the growth and distribution of the sessile algae in the River Hull, Yorkshire. *Jour. Ecol.* **28**: 210-223. 1940.
44. ———. Studies in the ecology of rivers. VI. Algal growth in certain highly calcareous streams. *Jour. Ecol.* **33**: 268-283. 1946.
45. ———. Studies in the ecology of rivers. VII. The algae of organically enriched water. *Jour. Ecol.* **35**: 186-191. 1947.
46. ———. Problems of distribution of sessile algae in running water. *Verh. Int. Ver. Theoret. Ang. Lim.* **10**: 98-103. 1949.
47. ———, LONGWELL, J., and PENTLOW, F. T. K. Survey of the river Tees. III. The non-tidal reaches—chemical and biological. *Dept. Sci. & Ind. Res. Water Poll. Res. Tech. Pap.* **6**. 2 frontisp. xii + 189 pp. 9 pl. 1937.
48. ———, PENTLOW, F. T. K., and WOODLEY, J. W. A. Variations in the composition of river waters. *Int. Rev. Ges. Hydrobiol. Hydrogr.* **24**: 47-80. 1930.
49. CEDERGRÉN, G. R. Reofila eller det rinnande vattnets algsamhällen. *Svensk Bot. Tidskr.* **32**: 362-373. 1938.

50. CHANDLER, D. C. Fate of typical lake plankton in streams. *Ecol. Monogr.* **7**: 445-479. 1937.
51. CHOLNOKY, B. v. Analytische Benthosuntersuchungen. *Arch. Hydrobiol.* **23**: 284-309. 1931; **26**: 207-254. 1933.
52. CHRISTJUK, P. M. Eine Wasserblüte am Don. *Aphanizomenon flos aquae*. *Mitt. Nordkaukas. Univ.* **11**: 49-51. 1926. [Not seen; cited in *Russ. Hydrobiol. Zeits.*]
53. CILLEULS, J. DES. Le phytoplancton de la Loire. *Compt. Rend. Acad. Sci. [Paris]* **182**: 649-651. 1926.
54. ———. Le phytoplancton du Thouet, affluent de la Loire. *Compt. Rend. Acad. Sci. [Paris]* **184**: 389-391. 1927.
55. ———. Revue générale des études sur le plancton des grands fleuves ou rivières. *Int. Rev. Ges. Hydrobiol. Hydrogr.* **20**: 174-206. 1928.
56. ———. Étude du phytoplancton des affluents de la Loire dans la région saumuroise. *Int. Rev. Ges. Hydrobiol. Hydrogr.* **22**: 179-231. 1929.
57. ———. Contribution nouvelle à l'étude du phytoplancton de la Loire. *Int. Rev. Ges. Hydrobiol. Hydrogr.* **27**: 120-129. 1932.
58. COFFING, CHARLENE. A quantitative study of phytoplankton of the White River canal, Indianapolis, Indiana. *Butler Univ., Bot. Stud.* **4**: 13-31. 1937.
59. COMÈRE, J. Observations sur la périodicité du développement de la flore algologique dans la région toulousaine. *Bull. Soc. Bot. France* **53**: 390-407. 1906.
60. CONGER, P. S. Aspects of the hydrobiological importance of diatoms. *In: Symposium on Hydrobiology.* 1941. [pp. 396-397].
61. CONRAD, W. Sur la faune et la flore d'un ruisseau de l'Ardenne belge. *Mém. Mus. Roy. Hist. Nat. Belg. I.* **99**: 1-177. Pl. 1, 2. 1942.
62. COWLES, R. P., and SCHWITALIA, A. M. The hydrogen ion concentration of a creek, its waterfall, swamp, and ponds. *Ecology* **4**: 402-416. 1923.
63. DENHAM, S. C. A limnological investigation of the West Fork and Common Branch of White River. *Invest. Indiana Lakes & Streams* **1**: 17-71. 1938.
64. DENIS, M. Une fleur d'eau sur la Mayenne. *Bull. de Mayenne-Sciences* **1921**: 1-3. 1 pl. 1921.
65. DJAKONOFF, F. F. Einige Beobachtungen über den Bewuchs an den Dampfern der unteren Wolga. *Arb. Biol. Wolga-Station* **8**: 135-156. 1925.
66. DOLGOFF, G. I. Über die Ungleichartigkeit des Flusswassers. *Int. Rev. Ges. Hydrobiol. Hydrogr.* **22**: 371-412. 1929.
67. DUVAL, M., and DUMARAND, R. Rapidité du changement de réaction des eaux de ruissellement. *Compt. Rend. Soc. Biol.* **89**: 231-236. 1923.
68. EDDY, S. Fresh water algal succession. *Trans. Amer. Microsc. Soc.* **44**: 138-147. 1925.
69. ———. A study of fresh-water plankton communities. *Ill. Biol. Monogr.* **12**: 1-93. 1934.
70. ELIASSEN, R. Stream pollution. *Sci. Amer.* **186**: 17-21. 1952.
71. ELLIS, M. M. Erosion silt as a factor in aquatic environments. *Ecology* **17**: 29-42. 1936.
72. FADEEV, N. N. Preliminary report of the sanitary-biological survey of the northern Donets basin, November 1924-April 1925. *Proc. Comm. Sanit.-Biol. Survey N. Donets and Trib. (Lopan and Ud)* Vol. 1: 3-12. 1926. [Not seen].
73. ———. Zur Methodik sanitär-biologischer Untersuchungen fließ-

- sender Gewässer. 1. Plankton oder Benthos? Russ. Hydrobiol. Zeits. 9: 22-45. 1930.
74. FJERDINGSTAD, E. The microflora of the River Mjølleaa with special reference to the relation of the benthic algae to pollution. Fol. Limnol. Scandinav. No. 5. 123 pp. 1 pl. 1950.
 75. FOGED, N. Diatoms in water courses in Funen. IV-VI. Dansk Bot. Ark. 12(9): 1-53 + 2 pp., *ibid.* (12): 1-110 + 2 pp. 1948.
 76. FORBES, S. A. The biological survey of a river system, its objects, methods, and results. Ill. Div. Nat. Hist. Survey 17: 277-284. 1928.
 77. FRIDMAN, G. M. [Materials for the study of the effect of industrial sewage on the bottom life of the River Kama.] Trav. Inst. Rech. Biol. Perm 8: 72-92. 1939.
 78. FRITSCHE, F. E. Further observations on the phytoplankton of the River Thames. Ann. Bot. 17: 631-647. 1903.
 79. ———. Algological notes. VI. The plankton of some English rivers. Ann. Bot. 19: 163-167. 1905.
 80. ———. Problems in aquatic biology with special reference to the study of algal periodicity. New Phytol. 5: 149-169. 1906.
 81. ———. The encrusting algal communities of certain fast-flowing streams. New Phytol. 28: 165-196. Pl. 5. 1929.
 82. ———. The structure and reproduction of the algae. Vol. I. xvii + 791 pp., frontisp. 1935. Vol. 2. xiv + 939 pp., frontisp., 2 maps. 1945.
 83. ———. The lime-encrusted *Phormidium*-community of British streams. Verh. Int. Ver. Theoret. Ang. Lim. 10: 141-144. Pl. 2. 1949.
 84. ———. *Phormidium incrustatum* (Näg.) Gom., an important member of the lime-encrusted communities of flowing water. Biol. Jaarboek 17: 27-39. Pl. 1, 2. 1950.
 85. GALTSOFF, P. S. Limnological observations in the upper Mississippi. U. S. Bur. Fish., Bull. 39: 347-438. 1924.
 86. GAUFIN, A. R., and TARZWELL, C. M. Environmental changes in a polluted stream during winter. Amer. Midl. Nat. 54: 78-88. 1955.
 87. GEITLER, L. Über einige häufige aber wenig bekannte Algen aus Gebirgsbächen. Mikrosk. für Naturfr. 15: 225-234. 1927.
 88. ———. Über Vegetationsfärbungen in Bächen. Biol. Gen. 3: 791-814. Pl. 18-21. 1927.
 89. GODWARD, MAUD B. An investigation of the causal distribution of algal epiphytes. Beih. Bot. Zentralbl. 52, A. 3: 506-539. 1934.
 90. GREZE, V. N. 1942. [Plankton of the Piasina River.] Zool. Zhurnal U.S.S.R. 21: 136-140. 1942.
 91. GUARRERA, SEBASTIAN A. Estudios hidrobiológicos en el Río de la Plata. Rev. Inst. Nac. Investig. Cienc. Nat. Cienc. Bot. 2: 1-62. 1950.
 92. GUIMARÃES, J. R. A. Considerações sobre a capacidade biogenica das águas. Rev. Indust. Animal (São Paulo) 1: 508-514. 1930.
 93. HAMEL, G. Le cours inférieur de la Rance. Bull. Mus. Hist. Nat. [Paris] 30: 414-416. 1924.
 94. HANOAKA, T. Hydrological and hydrobiological observation of Tikuma River. II. Contr. Centr. Fish. Sta. Japan 1946: 48-50. 1948.
 95. ———. Hydrological and hydrobiological observation of the Tikuma River. III. Contr. Centr. Fish. Sta. Japan 1946: 137-140. 1948.
 96. HERVEY, R. J. Effect of chromium on the growth of unicellular Chlorophyceae and diatoms. Bot. Gaz. 111: 1-11. 1949.
 97. HOPPOWNA, I. Plankton Warty pod Poznaniem. Poznańskie, Tow. Przyj. Nauk. Prace Kom. Mat.-Przyr. B. 3: 175-215. 1925.

98. HORNING, H. Biologischer Nachweis der Verunreinigung der Echaz durch Abwässer. Veröff. Landesst. Naturschutz Württemberg-Hohenzollern 1950: 272-280. 1951.
99. HUET, M. La Pollution des Eaux. L'analyse biologique des eaux polluées. Trav. Stat. Recherches Groenendaal. Tr. D. Bull. Centre Belge d'Etude et de Documentation des Eaux, No. 5, 6. 31 pp. 1949.
100. HUPP, E. R. Plankton and its relationship to chemical factors and environment in White River Canal, Indianapolis, Indiana. Butler Univ., Bot. Stud. 6: 30-50. 1943.
101. HUSTEDT, F. Diatomeen aus den Pyrenäen. Ber. Deut. Bot. Ges. 56: 543-572. 1939.
102. IRENÉE-MARIE, FR. Flore desmidiale de la région de Montréal. 547 pp. 1938.
103. ISRAELSON, G. On some attached Zygnemales and their significance in classifying streams. Bot. Not. 1949: 313-358. 1949.
104. ISSATCHENKO, B. À propos de deux cas de reproduction en masse de Cyanophycées. Rev. Alg. 1: 104-106. 1924.
105. IVLEV, V. S. Ein Versuch zur experimentellen Erforschung der Ökologie der Wasserbiocönosen. Arch. Hydrobiol. 25: 177-191. 1933.
106. IYENGAR, M. O. P., and VENKATARAMAN, G. The ecology and seasonal succession of the River Cooum at Madras with special reference to the Diatomaceae. Jour. Madras Univ. 21: 140-192. Pl. 1. 1951.
107. JAAG, O. 1938. Die Kryptogamenflora des Rheinfalls und des Hochrheins von Stein bis Eglisau. Mitt. Naturf. Ges. Schaffhausen 14: 1-158. Pl. 1-18. 1938.
108. JÄRNEFELT, H. Der Einfluss der Stromschnellen auf den Sauerstoff- und Kohlensäuregehalt und das pH des Wassers im Flusse Vuoksi. Verh. Int. Ver. Theoret. Ang. Lim. 10: 210-215. 1949.
109. JAO, C.-C. Studies on the fresh-water algae of China. XII. The attached algal communities of the Kialing River. Sinensia 15: 61-73. 1944.
110. JONES, H. Studies on the ecology of the River Rheidol. I. Plant colonization and permanent quadrat records in the main stream of the lower Rheidol. Jour. Ecol. 43: 462-476. 1955.
111. JÜRGENSEN, CHARLOTTE. Die Mainalgen bei Würzburg. Arch. Hydrobiol. 28: 361-414. Pl. 4-6. 1935.
112. KABANOV, N. M., NEIZWESTNOVA, K. S., and SASSUCHIN, D. N. Über die Sickerquellen der alluvialen Flussufer der Oka. Russ. Hydrobiol. Zeits. 7: 114-144. 1928.
113. KANN, EDITH. Über ein neues Vorkommen von *Chantransia incrustans* (Hansgirg) in Ostholstein. Beih. Bot. Zentralbl. 61(A): 120-124. 1941.
114. ———. Krustenalgen in Alpenbächen. Arch. Hydrobiol. 40: 459-473. 1943.
115. KEHR, R. W., PURDY, W. C., LACKEY, J. B., PLACAK, O. R., and BURNS, W. E. A study of the pollution and natural purification of the Scioto River. (U.S.A.) Public Health Bull. No. 276. xii + 153 pp. 1941.
116. KOFOID, C. A. The plankton of the Illinois River, 1894-1899, with introductory notes upon the hydrography of the Illinois River and its basin. Part I. Quantitative investigations and general results. Bull. Ill. State Lab. Nat. Hist. 6: 95-629. pl. 1-50. 1903.
117. ———. The plankton of the Illinois River, 1894-1899, with introductory notes upon the hydrography of the Illinois River and its basin. Part II. Constituent organisms and their seasonal distribution. Bull. Ill. State Lab. Nat. Hist. 8: i-vii, 1-355. Pl. 1-5. 1908.

118. KOLBE, R. W. Grundlinien einer allgemeinen Ökologie der Diatomeen. *Ergebn. Biol.* **8**: 221-348. 1932.
119. KOLKOWITZ, R. Die Beziehungen des Kleinplanktons zum Chemismus der Gewässer. *Mitt. Kgl. Prüfungsanst. Wasserversorgung Abwärserbeseitigung* **14**: 145-215. 1911.
120. ———. Zur Ökologie der Saprobien. *Runds. Deuts. Bot. Ges.* **1946**: 10. 1946.
121. ———. Ökologie der Saprobien. Über die Beziehungen der Wasserorganismen zur Umwelt. *Schriftenr. Ver. Wasser-, Boden-, Lufthyg.* No. 4. 64 pp. 1950.
122. ——— and MARSSON, M. Oekologie der pflanzlichen Saprobien. *Ber. Deut. Bot. Ges.* **26a**: 505-519. 1908.
123. KRIEGER, W. Zur Biologie des Flussplanktons. Untersuchungen über das Potamoplankton des Havelgebietes. *In*: R. Kolkowitz, *Pflanzenforschung* **10**. vi, 66 pp., 5 pl. 1927.
124. KURZ, A. Grundriss einer Algenflora des appenzellischen Mittel- und Vorderlandes. *Jahrb. St. Gall. Naturwiss. Ges.* **58**, II: 67-152. Pl. 1, 2. 1922.
125. LACKEY, J. B. The flora and fauna of surface waters polluted by acid mine drainage. (U.S.A.) *Public Health Rep.* **53**: 1499-1507. 1938.
126. ———. Aquatic life in waters polluted by acid mine waste. (U.S.A.) *Public Health Rep.* **54**: 740-746. 1939.
127. ———. The significance of plankton in relation to the sanitary condition of streams. *In*: *A Symposium on Hydrobiology.* 1941. [pp. 311-328].
128. ———. The effects of distillery wastes and waters on the microscopic flora and fauna of a small creek. (U.S.A.) *Public Health Rep.* **58**: 253-260. 1942.
129. ———. The plankton algae and protozoa of two Tennessee rivers. *Amer. Midl. Nat.* **27**: 191-202. 1942.
130. ———, WATTIE, ELSIE, KACHMAR, J. F., and PLACAK, O. R. Some plankton relationships in a small unpolluted stream. *Amer. Midl. Nat.* **30**: 403-425. 1943.
131. LASTOCHKIN, D. Achievements in Soviet hydrobiology of continental waters (ed. G. E. Hutchinson). *Ecology* **26**: 320-331. 1945.
132. LAUTERBORN, R. Über das Vorkommen der Diatomeen-Gattungen *Atheya* und *Rhizosolenia* in den Altwässern des Oberrheins. *Ber. Deut. Bot. Ges.* **14**: 11-15. 1896.
133. ———. Die Vegetation des Oberrheins. *Verh. Naturhist.- Mediz. Ver. Heidelberg.* n.F. **20**: 450-502. 1910.
134. ———. Die geographische und biologische Gliederung des Rheinstroms. *Sitzber. Heidelberg. Akad. Wiss. Klasse 7B (Biol. Wiss.)* (6): 1-61. 1916; **8B**(5): 1-70. 1917; **9B**(1): 1-87. 1918.
135. LEFÈVRE, M. Influence des déversements d'eaux usées de la région parisienne sur le plancton de la Seine. *Ann. Sta. Centr. d'Hydrobiol. Appl.* **3**: 153-171. 1950.
136. LEMMERMANN, E. Das Plankton der Weser bei Bremen. *Arch. Hydrobiol. Planktonk.* **2**: 393-447. 1907.
137. LIEBMANN, H. 1942. Über den Einfluss der Verkrautung auf den Selbstreinigungsvorgang in der Salle unterhalb Hof. *Vom Wasser* **14**: 92-102. 1942.
138. LIMANOWSKA, HEDWIG. Die Algenflora der Limmat. *Arch. Hydrobiol. Planktonk.* **7**: 331-408, 523-594. pl. 1. 1912.
139. LIST, H. Die Entwicklungsgeschichte von *Cladophora glomerata* Kützing. *Arch. Protistenk.* **72**: 453-481. 1930.
140. LONGWELL, C. R., KNOPF, A., and FLINT, R. F. *A text-book of geology.* Vol. 1. Physical geology. vii, 514 pp. 1932.

141. LUTHER, H. Vorschlag zu einer ökologischen Grundeinteilung der Hydrophyten. *Acta Bot. Fenn.* **44**: 1-15. 1949.
142. ———. Über Krustenbewuchs an Steinen fließender Gewässer, speziell in Sudfinnland. *Acta Bot. Fenn.* **55**: 1-61. 1954.
143. MACAN, T. T., and WORTHINGTON, E. B. Life in lakes and rivers. xvi, 272 pp. 72 pl. 1951.
144. MARGALEF, R. Las asociaciones de algas en las aguas dulces de pequeño volumen del Noreste de España. *Vegetatio* **1**: 1948(49): 258-284. 1949.
145. ———. A new limnological method for the investigation of thin-layered epilithic communities. *Hydrobiologia* **1**: 215-216. 1949.
146. ———. Datos para la hidrobiología de la cordillera cantábrica, especialmente del macizo de los Picos de Europa. *Publ. Inst. Biol. Aplicada [Barcelona]* **7**: 37-76. 1950.
147. MATTHEWS, VELMA D. The aquatic vegetation of Quaker Run. *Jour. Elisha Mitchell Sci. Soc.* **47**: 74-84. 1932.
148. MEYER, K. Das Phytoplankton des Flusses Oka bei Murom in den Jahren 1919-1921. *Arb. Biol. Oka-Stat. Murom* **2**: 13-61. 1923.
149. ———. Introduction to the algological flora of the River Oka and its valley. I. The Oka. *Arb. Biol. Oka-Stat. Murom* **5**: 4-53. 1928.
150. MÜLLER, K. Die Drift in fließenden Gewässern. *Arch. Hydrobiol.* **49**: 539-545. 1954.
151. MUTKOWSKI, R. A. The ecology of trout streams in Yellowstone National Park. *Roosevelt Wildlife Ann.* **2**: 154-240. 1929.
152. NEEDEHAM, J. G., and CHRISTENSON, R. O. Economic insects in some streams of northern Utah. *Utah Agr. Exp. Sta., Bull.* **201**. 36 pp. 1927.
153. NEEDEHAM, P. R. Bottom foods in trout streams. *Field & Stream* **36**(2): 40-44. 1932.
154. NEEL, J. K. Interrelations of certain physical and chemical features in a headwater limestone stream. *Ecology* **32**: 368-391. 1951.
155. NORRINGTON, A. Phycological study of some of the mountain lakes and streams of the Wasatch and Uinta Ranges in Utah. *Abstr. Theses, Univ. Chic., Sci. Ser.* **3**: 287-292. 1927.
156. NOWAK, W. Über die Verunreinigung eines kleinen Flusses in Mähren durch Abwässer von Weissgerbereien, Leder-, Leimfabriken und anderen Betrieben. *Arch. Hydrobiol.* **36**: 386-423. Pl. 12-15. 1940.
157. OLSON, R. A., BRUST, H. F., and TRESSLER, W. L. Studies of the effects of industrial pollution in the lower Patapsco River area. I. The Curtis Bay Region, 1941. *Chesapeake Biol. Lab. Public. No.* **43**. 40 pp.
158. OLTMANN, F. *Morphologie und Biologie der Algen*. 2 Aufl. 3 vols. 1922-23.
159. OYE, P. VAN. Zur Biologie des Potamoplanktons auf Java (2 Aufsatz). *Int. Rev. Ges. Hydrobiol. Hydrogr.* **12**: 48-59. 1924.
160. ———. Le potamoplancton du Ruki au Congo-belge et des pays chauds en général. *Int. Rev. Ges. Hydrobiol. Hydrogr.* **16**: 1-50. 1926.
161. PANKNIN, W. Die Vegetation einiger Seen in der Umgebung von Joachimsthal. *Bibl. Bot. H.* **119**. vii, 162 pp. 1941.
162. ———. Zur Entwicklungsgeschichte der Algensoziologie und zum Problem der "echten" und "zugehörigen" Algengesellschaften. *Arch. Hydrobiol.* **41**: 92-111. Pl. 10-12. 1945.
163. PATRICK, RUTH. A proposed biological measure of stream conditions, based on a survey of the Conestoga Basin, Lancaster County, Pennsylvania. *Proc. Acad. Nat. Sci. Phila.* **101**: 277-344. 1949.

164. ———, HOHN, M. H., and WALLACE, J. H. A new method for determining the pattern of the diatom flora. Not. Naturae No. 259. 12 pp. 1954.
165. PEARSALL, W. H. A theory of diatom periodicity. Jour. Ecol. 11: 165-183. 1923.
166. ——— (ed.) Biological survey of the River Wharfe. Jour. Ecol. 18: 273-305. 1930.
167. PENTELOW, F. T. K., BUTCHER, R. W., and GRINDLEY, J. An investigation of the effects of milk wastes on the Bristol Avon. Min. Agr. Fish., Fishery Invest. I. 4(1): 1-76. Pl. 1-3. 1938.
168. PIA, J. Kohlensäure und Kalk. Einführung in das Verständnis ihres Verhaltens in den Binnengewässern. In: A. Thienemann, Die Binnengewässer, Bd. 13. 183 pp. 3 pl. 1933.
169. PICKEN, L. E. R. Mechanical factors in the distribution of a blue-green alga, *Rivularia haematites*. New Phytol. 35: 221-228. 1936.
170. PORETZKII, V. S. Beobachtungen über das Diatomeen-plankton des Flusses Grosse Nevka (Leningrad) im Winter 1923-24. Russ. Hydrobiol. Zeits. 4: 201-213. 1925.
171. ———. [Life in the Botanic Garden Park as related to the flood of September 23, 1924.] Russ. Hydrobiol. Zeits. 5: 182-188. 1926.
172. POWERS, E. B. The carbon dioxide tension, oxygen content, the pH and the alkali reserve of natural waters mostly of the western portion of the United States. Puget Sound Biol. Sta., Publ. 5: 381-391. 1928.
173. PRÁT, S. Studie o Biolithogenesi. 187 pp. 13 pl. 1929.
174. PRINGSHEIM, E. G., and PRINGSHEIM, OLGA. The growth requirements of *Porphyridium cruentum*: with remarks on the ecology of brackish water algae. Jour. Ecol. 37: 57-64. 1949.
175. PURDY, W. C. Potomac plankton and environmental factors. In: Cumming, H. S. Investigation of pollution and sanitary conditions of the Potomac watershed with special reference to self purification and the sanitary condition of shellfish in the lower Potomac River. (U.S.A.) Hygienic Lab. Bull. Publ. Health Serv. No. 104, pp. 130-191. 1916.
176. ———. A study of the pollution and natural purification of the Illinois River. II. The plankton and related organisms. (U.S.A.) Public Health Bull. No. 198. xvi, 212 pp. 1930.
177. QUIRMBACH, J. Studien über das Plankton des Dortmund-Emskanals und der Werse bei Münster. Arch. Hydrobiol. Planktonk. 7: 409-474, 595-636. 1912.
178. RAABE, HILDEGARD. Die Diatomeenflora der ostholsteinischen Fließgewässer. Arch. Hydrobiol. 44: 521-638. 1951.
179. RABANUS, A. Beiträge zur Kenntnis der Periodizität und der geographischen Verbreitung der Algen Badens. Inaug.-Dissert. Albert-Ludwigs Univ. Freiburg i. Br. iii, 1, 158 pp. 2 pl. 1915.
180. RADISCHTSHEV, W. P. Über die Schwefelstoffe des Wolgawassers bei Saratow. Arb. Biol. Wolga-Stat. 8: 116-124. 1925.
181. ———. Über die jährlichen Veränderungen in der chemischen Zusammensetzung des Wolgawassers bei Saratow. Arb. Biol. Wolga-Stat. 8: 229-266. 1926.
182. RADZIMOVSKII, D. O. [The microflora of water in the Kiev region.] Acad. Sci. Ukraine, Mém. Cl. Sci. Phys. Math. (Trav. Sta. Biol. Dniepre 3) 10: 99-112. 1928.
183. RAVERA, O. Velocità di corrente e insediamenti bentonici. Studio su una lanca del fiume Toce. Mem. Ist. Ital. Idrobiol. Dott. Marco de Marchi 6: 221-267. 1951.

184. REESE, MARY J. Report on the microflora of the Rheidol and Melindwr above and below sources of pollution by lead mines. Min. Agr. Fish. Ser. 123, Rep. 510. 17 pp. 1935.
185. ———. The microflora of the non-calcareous streams Rheidol and Melindwr with special reference to water pollution from lead mines in Cardiganshire. Jour. Ecol. **25**: 386-407. Pl. 21. 1937.
186. REIF, C. B. The effect of stream conditions on lake plankton. Trans. Amer. Micros. Soc. **58**: 398-403. 1939.
187. REINHARD, E. G. The plankton ecology of the upper Mississippi, Minneapolis to Winona. Ecol. Monogr. **1**: 395-464. 1931.
188. RICE, C. H. Studies in the phytoplankton of the River Thames (1928-1932) I. Ann. Bot. n.s. **2**: 539-557. II. *ibid.* 559-581. 1938.
189. RICHARDSON, R. E. The bottom fauna of the Middle Illinois River, 1913-1925. Ill. Nat. Hist. Survey, Bull. **17**: 387-475. 1928.
190. RICKER, W. E. An ecological classification of certain Ontario streams. Univ. Toronto Stud., Biol. Ser. **37**: 1-114. 1934.
191. ROACH, L. S. An ecological study of the plankton of the Hocking River. Bull. Ohio Biol. Survey **5**: 253-279. 1932.
192. ROBERG, M. Ein Beitrag zur Stoffwechselphysiologie der Grünalgen. II. Über die Wirkung von Eisen-, Zink- und Kupfersalzen. Jahrb. Wiss. Bot. **76**: 311-332. 1932.
193. ROLL, H. Die Pflanzengesellschaften ostholsteinischer Fließgewässer. Arch. Hydrobiol. **34**: 159-305. 1938.
194. ———. Neue Pflanzengesellschaften aus ostholsteinischen Fließgewässern. Beih. Bot. Zentralbl. **58B**: 466-475. 1938.
195. ROSENTHAL, M. Das Kammerplankton der Spree bei Berlin. Int. Rev. Ges. Hydrobiol. Hydrogr. Biol. Suppl. **6**(2): 1-22. 1914.
196. ROY, H. K. Plankton ecology of the River Hooghly at Palta, West Bengal. Ecology **36**: 169-175. 1955.
197. RUTTNER, F. Fundamentals of limnology. Transl. from German by D. G. Frey and F. E. J. Fry. xi, 242 pp. 1953.
198. SCHALLGRUBER, F. Das Plankton des Donaustromes bei Wien in qualitativen und quantitativen Hinsicht. Arch. Hydrobiol. **39**: 665-689. 1944.
199. SCHEELE, M. Systematisch-ökologische Untersuchungen über die Diatomeenflora der Fulda. Arch. Hydrobiol. **46**: 305-423. 1952.
200. ———. Die Diatomeenflora der Schleusenwände in der unteren Fulda und die Lichtabhängigkeit einiger Diatomeenarten. Arch. Hydrobiol. **49**: 581-589. 1954.
201. ———. Die Massenentwicklung salzliebender planktischer Kieselalgenarten in Werra und Weser. Arch. Hydrobiol. **51**: 161-171. 1955.
202. SCHLJAPINA, E. Über den Diatomeenbewuchs der Simuliidenbiocoenose in der Wolga. Russ. Hydrobiol. Zeits. **5**: 196. 1926.
203. SCHMASSMANN, H. Die Stoffhaushalts-Typen der Fließgewässer. Arch. Hydrobiol. Suppl. **22**: 504-509. 1955.
204. SCHORLER, B. Mitteilungen über das Plankton der Elbe bei Dresden im Sommer 1904. Arch. Hydrobiol. Planktonk. **2**: 355-357. 1907.
205. SCHRÖDER, B. Planktologische Mitteilungen. Biol. Zentralbl. **18**: 525-535. 1898.
206. ———. Das pflanzliche Plankton der Oder. Forschungsber. Biol. St. Plön **7**: 15-24. 1899.
207. SCHRÖDER, H. Die Algenflora der Mulde. Ein Beitrag zur Biologie saprober Flüsse. In: R. Kolkwitz, Pflanzenforschung **21**. vi, 88 pp. 1 pl. 1939.
208. SCHUTOFF, D. A. Materialien zur Flora der Grünalgen des Wolgaplanktons. Arb. Biol. Wolga-Stat. **6**(4): 215-232. Pl. 1-3. 1922.
209. SEELER, T. Über eine quantitative Untersuchung des Planktons der

- deutschen Ströme unter besonderer Berücksichtigung der Einwirkung von Abwässern und der Vorgänge der biologischen Selbstreinigung. Arch. Hydrobiol. 28: 323-356. 1935.
210. SHELFORD, V. E., and EDDY, S. Methods for the study of stream communities. Ecology 10: 382-391. 1929.
 211. SIOLI, H. Beiträge zur regionalen Limnologie des Amazonasgebietes. Arch. Hydrobiol. 49: 441-518. 1954.
 212. SMITH, G. M. The fresh-water algae of the United States. 2 ed. vii, 719 pp. 1950.
 213. SÖRENSEN, I. Biological effects of industrial defilements in the River Billebergaån. Acta Lim. 1: 73 pp. 1948.
 214. STARMACH, K. Badania sestonu górnej Wisły i Białej Przemszy. Osobne Odb. Spraw. Kom. Fizjogr. Polsk. Akad. Umiej. 73: 145 pp. 6 pl. 1938.
 215. STARRETT, W. C., and PATRICK, RUTH. Net plankton and bottom microflora of the Des Moines River, Iowa. Proc. Acad. Nat. Sci. Phila. 104: 219-243. 1952.
 216. STEUER, A. Planktonkunde. xv, 723 pp. 1910.
 217. STRØM, K. M. Studies in the ecology and geographical distribution of fresh water algae and plankton. Rev. Algol. 1: 127-155. 1924.
 218. ———. Norwegian mountain algae. Skr. Norsk. Vid.-Akad. Oslo I. Mat.-Nat. Kl. 2: 1-264. Pl. 1-25. 1927.
 219. SUMMERHAYES, V. S., and ELTON, C. S. Contributions to the ecology of Spitsbergen and Bear Island. Jour. Ecol. 11: 214-286. 1923.
 220. SWIRENKO, D. Plankton of the lower Dniester. Ber. Wiss. Forsch.-Inst. Odessa 2(4): 21-40. 1926.
 221. SYMOENS, J. J. Esquisse d'un système des associations algales d'eau douce. Verh. Int. Ver. Theoret. Ang. Lim. 11: 395-408. 1951.
 222. TARNAVSKI, I. T. Über *Hildenbrandia rivularis* (Liebm.) J. Agardh und ihr Vorkommen in Rumänien mit Berücksichtigung ihrer Verbreitung in Europa. Bull. Sect. Sci. Acad. Roumanie 24: 259-272. 1943.
 223. TAYLOR, W. R. The cryptogamic flora of the Arctic. Bot. Rev. 20: 363-399. 1954.
 224. THIENEMANN, A. Die Binnengewässer Mitteleuropas. In: A. Thienemann, Die Binnengewässer. Bd. I. 255 pp. 1925.
 225. THURMAN, MARTHA H., and KUEHNE, R. A. An ecological study of *Cladophora glomerata* (Chlorophyceae) near Dallas. Field & Lab. 20: 26-28. 1952.
 226. TIFFANY, L. H. The ecology of freshwater algae. In: G. M. Smith, Manual of phycology. 1952. [pp. 293-341].
 227. TRANSEAU, E. N. The periodicity of fresh water algae. Amer. Jour. Bot. 3: 121-133. 1916.
 228. United States Public Health Service, Ohio River Pollution Control. Biological studies. In: House Doc. 266, 78th Congress of U. S. A., 1st Sess., Rep. U. S. Publ. Health Serv., Suppl. F: 1275-1368. 1944.
 229. USPENSKI, E. E. Eisen als Faktor für die Verbreitung niederer Wasserpflanzen. In: R. Kolkwitz, Pflanzenforschung 9: vi, 104 pp. 1927.
 230. VIVIER, P. La vie dans les eaux douces. 128 pp. 1946.
 231. ——— and URBAIN, P. Étude sur les repercussions nocives à distance des déversements industriels d'une usine de viscosse. Ann. Sta. Centr. Hydrobiol. Appl. 2: 9-17. 4 pl. 1948.
 232. VOLK, R. Mitteilungen über die biologische Elbe-Untersuchung des Naturhistorischen Museums in Hamburg. Verh. Naturwiss. Ver. Hamburg 3 fol. 15: 1-54. Pl. 1-3. 1908.

233. WASER, E., BLÖCHLIGER, G., and THOMAS, E. A. Untersuchungen am Rhein von Schaffhausen bis Kaiserstuhl 1938-1939 und 1940-1941. Zeits. Hydrol. 9: 225-309. 1943.
234. WEHRELE, E. Algen in Gebirgsbächen am Sudostrande des Schwarzwaldes. Beitr. Naturk. Forsch. Oberrheingebiet 7: 128-286. Pl. 1-3. 1942.
235. WELCH, P. S. Limnology. 2 ed. xi, 558 pp. 1952.
236. WHIPPLE, G. C. The microscopy of drinking water. Rev. by Fair, G. M. and Whipple, M. C. 4 ed. 2 p. iii, xix, 86 pp. 20 pl. 1927.
237. WIEBE, A. H. Biological survey of Upper Mississippi with special reference to pollution. Bull. U. S. Bur. Fish. 43(2): 137-167. 1928.
238. WOOD, R. D., and STRAUGHAN, JEANETTE. Time-intensity tolerance of *Lemanea fucina* to salinity. Amer. Jour. Bot. 40: 381-384. 1953.
239. WORONOCIN, N. Algen des Polar- und des Nord-Urals. Trud. Leningradsk. Obshchest. Estestv. 60: 3-77. Pl. 1-3. 1930.
240. ———. Zur Kenntnis der Algenflora und Algenvegetation in den Süßwasserbecken der Krim. Jour. U. R. S. S. 17(3): 265-325. 1932.
241. WU, YI FANG. A contribution to the biology of *Simulium* (Diptera). Pap. Mich. Acad. Sci., Arts, Lett. 13: 543-599. 1931.
242. WYSOCKA, HANNA. Algues de la Vistule au rayon de Varsovie I. Acta Soc. Bot. Polon. 20: 69-118. 1950. II. *Ibid.* 21: 369-400. 1952.
243. ZACHAROW, N. D. A., and HENCKEL, P. Beobachtungen über den Einfluss einiger äusseren Umständen auf *Cladophora glomerata*. Bull. Inst. Res. Biol. Sta. Univ. Perm 2: 343-348. 1 pl. 1924.