

CHAPTER 4. Ecology: Distribution and Abundance

What is known of the occurrence of the Saprolegniaceae in relation to particular environmental factors was the chief message in the preceding chapter. At this point we consider those investigations dealing with the ecological distribution¹ and abundance¹ of these fungi in major habitat types: lakes, ponds, or streams (and their sediments), and soil. The subject matter is varied: distribution of water molds in relation to vascular plant communities, vertical and lateral distribution, and their occurrence in polluted water, to name a few considerations. Precisely which reports to include under the heading of distribution and abundance is an arbitrary decision, and is perhaps less important than the question: what is the part played by the water molds in the habitats where they occur? Unfortunately, that question still has no answers.

It has been emphasized on more than one occasion (Park, 1972a, b; Dick, 1971c, 1976) that mere isolation of a species provides no data as to its origin or potential activity in the site from which it came (Newton, 1971, appears to have some contradictory evidence). In any event, it is essential that a goal for ecological research will be to identify each individual species as to the niche it occupies in a given habitat. Furthermore, it must be recognized that the impact of the varied elements in any given habitat -- the biota and a host of edaphic and hydrographic factors -- is probably not unidirectional; the water molds very likely contribute formatively to their habitat as well as receive its benefits. Some models have been advanced to serve in the capacity of niche identification. They predictably fall short of accomplishing this task because they do not propose how the identification is arrived at. We discuss the models in the following section, but without any attempt to give prominence to any suspected ecological activity of the fungi themselves. To accord eminence to their activity would be to make too much of severely limited observations, measurements, and data. Nevertheless, it is well to bear these models in mind as the results of published research are pondered.

ECOLOGICAL NICHE MODELS

While Dick (1971c, 1976), and Park (1972b) have been most explicit about ecological activity of zoosporic fungi, they cannot be credited with being the first to speculate on the role of these fungi (including the Saprolegniaceae) in their natural habitats. This distinction goes to Weston (1941). He hypothesized that zoosporic fungi were probably passive members of the soil community as opposed to being active ones in an aquatic environment. Thirty years later Newton (1971) was to demonstrate experimentally to her satisfaction (washing to remove casual spores) that saprolegniaceous fungi actually attach to and grow in leaves submerged in a natural body of water. As she expressed it, leaf material put into a river "attracts" a number of fungal colonists, among them some water molds.

The niche model advanced by Dick (1971c) was limited to the lentic and lotic habitat, and was essentially a unidirectional one for those organisms he considered to be "aliens." In effect his model proposed that there were two segments of the

¹ Defined in an ecological sense in Chapter 3.

aquatic mycoflora, the aliens and the inhabitants, the difference being found in their origin. The aliens entering the aquatic system as propagules from terrestrial reservoirs, for example, were unable to maintain themselves in the aquatic habitat (Dick, 1976), and thus were either washed out of it, or became a part of the detritus. Dick conceived of an active alien as one capable of growing and sporulating in the aquatic system, but destined to have no permanence there.

Park's (1972b) model of the origin of microorganisms in an aquatic system has been termed "cyclic" by Dick (1976), but it seems no more cyclic than Dick's (1971c) own hypothetical model. According to Park, the members of the aquatic microbiota originate either as indwellers or immigrants. The former acquire a degree of ecological adaptation enabling them to maintain themselves as permanent residents year to year as a relatively constant biomass. Immigrant species (Park, 1972b) originate outside the aquatic system, and are of two types. The migrants periodically alternate between an aquatic and nonaquatic habitat; the versatiles move between these two habitat types in a haphazard fashion. The chief thread in Park's model differs not at all from that in Dick's, since both recognized that some individuals entering an aquatic system were transients, declining immediately upon arrival or after some interval of time because of their inability to adapt to the particular environment and community. It must not be concluded -- and in this we are in agreement with Park -- that an immigrant (alien or transient) which must be renewed periodically from outside the aquatic system to be able to occupy a niche there is not a contributor. Precisely what role these "non-dwellers" play is yet to be determined, but they are probably not inert.

ECOLOGICAL DISTRIBUTION IN AQUATIC SYSTEMS

Two major approaches have been taken in research to determine ecological distributional patterns of saprolegnians in lakes. Some investigations sought answers to this somewhat general question: how abundant are these fungi in particular regions or communities in lakes? Others have inquired into the vertical distribution of water molds in aquatic habitats.

GENERAL DISTRIBUTION IN LAKES AND PONDS

The conclusion that emerges from Manoharachary's (1974) study on some Indian water molds is that these fungi are more abundant in water than in sediments or shoreline soils. Only one species, *Achlya recurva*, occurred in all three habitats, and no species of *Saprolegnia* were recovered at all. Mer *et al.* (1980) reported being able to group the species they collected into three categories: aquatic, amphibious, and terricolous. In general, they reported that species with eccentric oospores were more frequent in soils while those with centric oospores were most frequently found in water.

Much of the work by Suzuki (and associates) simply determined (by counts of zoospores in samples; Chapter 3) the abundance of particular species in various lake systems (Suzuki, 1962a, b; Suzuki and Nimura, 1961d; Suzuki and Nishita, 1963). For example, Suzuki (1960a) stated that the numbers of water mold spores declined as samples were taken successively from points on the shoreline out to what he termed the

“disharmonic” portion of lakes (Suzuki, 1960e). Spores were very abundant (Suzuki, 1960e) in eutrophic lakes, but scarce in mesotrophic and oligotrophic ones, and in some so-called disharmonic lakes Suzuki (1961e) found no watermold spores,

Some studies of the ecological distribution of Saprolegniaceae have yielded only rather general data. Bock (1956) found in one lake system that an unidentified *Aphanomyces* was more abundant (its frequency -- not statistically verified -- was determined by the number of samples in which it occurred) than a nonsexual *Achlya* and a *Saprolegnia* he tentatively identified as *S. variabilis*[†]. The report of watermolds by Gaertner and Sparrow (1966) in some Michigan lakes shows these fungi to have no distributional patterns, but this could well be due to very limited frequency and extent of collecting, or to the effect of experimental design.

Just as had V. G. Collins and Willoughby (1962), Willoughby (1962, 1965) recovered many more propagules of saprolegniaceous fungi in surface water at the shoreline than in the center of certain English lakes. Yields from one lake (Willoughby, 1962) suggested that a correlation existed between rainfall and numbers of propagules. During periods of high rainfall, with a subsequent rise in the lake level, the numbers of watermold propagative units were also high. At Blelham Tarn (England) Willoughby and Collins (1966; see also Willoughby, 1968a) established a series of sampling stations at points leading into and from the lake and in the lake itself. Although no particular qualitative differences were evident among the watermolds recovered from the various stations, there was a definite quantitative difference. The spores of fungi other than watermolds were distributed relatively homogeneously in the surface water, whereas those of members of the Saprolegniaceae were more abundant in water at the lake margins than in its center. Willoughby and Collins suggested that the spore load in the waters at the lake center was reinforced by that developed at the shoreline. Dick's (1971c) study of the quantitative abundance (density) of watermolds in sediments -- a significant parallel to the investigations by V. G. Collins and Willoughby (1962), Willoughby (1962), and Willoughby and Collins (1966) -- is treated in a subsequent section.

VERTICAL DISTRIBUTION IN LAKES

There are a number of accounts relating ecological distribution and abundance of species of Saprolegniaceae to the depth of water in lakes and ponds. Among the first of such reports was that by Höhnk and Bock (1954). They sampled a lake at various depths (before and after thermocline development) along two intersecting transects. The species they collected could be distributed into three of the groups proposed by Höhnk (1935a) on the basis of the manner of sporulation. These groups are (following Höhnk's designations): II -- the *Saprolegnia* type (species of *Saprolegnia*, *Isoachlya*, and *Leptolegnia*), III -- the *Achlya* type (representatives of *Achlya* and *Aphanomyces*), and IV -- the *Dictyuchus* type. Prior to the thermocline, representatives of group II were limited to the upper half of the lake's water, spores of *Dictyuchus* species (IV) occurred only from the surface to a depth of about two meters, while the *Achlya*-*Aphanomyces* sporulation group (III) was distributed throughout the lake at all depths. After the thermocline had been established, species with sporulation types II and III were distributed vertically to about the same depth as the thermocline. Representatives of

Dictyuchus, on the other hand, were still limited to surface and near-surface waters, but were more abundant after the thermocline was in position than prior to its establishment. In summary, the data (not supported by statistical analyses) provided by Höhnk and Bock (1954) indicate that those fungi with a *Saprolegnia* type of sporulation were limited distributionally in the lake by a sharp lower boundary both before and after the thermocline developed; those of the *Achlya* type were sharply restricted vertically only after the thermocline was in place.

The results of studies by Suzuki and Hatakeyama (1960) and Suzuki and Nimura (1961c) do not entirely agree with those reported by Höhnk and Bock (1954). In certain Japanese lakes spores (from species of *Achlya*, *Saprolegnia*, *Aphanomyces*, *Leptolegnia*, and *Thraustotheca*) were distributed uniformly during the water's circulation (overturn) period, with those of species of *Saprolegnia* being most frequent in surface and near-surface waters. Spores of members of *Achlya* and *Aphanomyces* appeared more frequently in samples from deep waters. From collections in another series of lakes, however, Suzuki (1960e) noted that the distribution of the population of *Aphanomyces* species did not extend below the thermocline. Other records of vertical distribution of planonts -- Suzuki (1960a, d, e; 1961d; 1962b), and Suzuki and Hatakeyama (1961) -- indicate that some species, at some seasons, were virtually surface dwellers while at other seasons (related to oxygen level; see Chapter 3) they were distributed widely as to depth.

Paterson (1967) assembled data on the benthic distribution of two groups of zoosporic fungi in Lake Michigan and in a much smaller lake in northern Michigan. In the small lake he found approximately three times as many chytrids as oomycetous species, but the reverse was true for collections in Lake Michigan where he recovered four times more species of the latter than of the former. This single investigation, though interesting, was not sufficiently extensive to permit any sound inferences to be drawn from it.

Only specimens belonging to the genus *Leptolegnia* (presumed to be only one species, according to Dick, communication) colonizing exuviae displayed any distribution pattern with respect to water depth (Dick, 1970). The remainder of the data in his account on occurrence and abundance of water molds on exuviae show that some species are more frequent inhabitants of such a substratum than are others. There is, however, a discernible suggestion of a substrate preference: species of *Saprolegnia* were most frequent on exuviae of trichopterans, while members of *Achlya* and *Leptolegnia* were most commonly collected on the cast integuments of anisopterans (Dick, 1970).

DISTRIBUTION IN LAKE AND STREAM SEDIMENTS

Patterns of water mold distribution in sediments of certain Japanese lakes -- as reflected in counts of hyphae -- do not show any consistency or trends (Suzuki, 1961b, e, h, 1962b; Suzuki and Hatakeyama, 1961; Suzuki and Nimura, 1961a, d). Sampling in a series of shallow (1-1.5 m) lakes Suzuki and Nimura (1961d) found only one species in the water, but 90-100% of samples from sediments yielded water molds. In other lake systems, on the contrary, there were consistently fewer members of the family isolated from bottom sediments than from the overlying water, and none was found in the bottom muds of some lakes. Still other bodies of water yielded from their sediments

very scanty numbers of Saprolegniaceae in samples taken during summer months, but large numbers in mid-winter samplings (Suzuki, 1961b; Suzuki and Hatakeyama, 1961).

Some English lakes have also been examined ecologically for the occurrence and abundance of water molds in bottom sediments. Not one member of the Saprolegniaceae was isolated by V. G. Collins and Willoughby (1962) from bottom muds either at the margin or center of Blelham Tarn. In a later investigation of fungi in the same lake, Willoughby (1965) calculated that there were 320-1300 water mold propagules L⁻¹ bottom sediments, but soils at the shore of the lake yielded propagules in the range of >8000-150,000 L⁻¹ (samples frequently dominated by *Aplanopsis spinosa*[†]). These numbers, arrived at by Willoughby's method of quantifying isolates from samples (Chapter 3), are vastly different from those Suzuki recorded by counting hyphae appearing on hempseed bait. The latter seldom reported numbers of propagules higher than 100-400 10 mL⁻¹ of water (10,000-40,000 L⁻¹) and counts as high as 1800 10 mL⁻¹ (180,000 L⁻¹) indeed seemed to be unusual. Meaningful comparisons between Suzuki's studies and those of Willoughby are impossible because of the very different methods used to arrive at their numerical data.

Brief mention must be made of the one study designed specifically to assay the distribution of water molds in river bottom sediments (Fajola *et al.*, 1978). Sampling stations were established along shaded (presumably a heavy tree canopy) and unshaded zones of rivers. The sediment was either baited directly when collected, or first diluted, or was washed to remove the organic detritus before baiting. Some species -- *Achlya dubia*, *Dictyuchus anomalus*[†] and *Saprolegnia litoralis*, for example -- were uniformly distributed among the sampling stations. There were, however, more species recovered from sediments taken in the shaded zones of the rivers than from those collected in the open or exposed zones. No direct explanation is offered to account for this difference in composition. The shaded zones perhaps provided more organic matter to the river bottom than did the open regions, and these organically rich areas were more favorable for the development of water molds (drifting of materials from one zone to the adjacent one is not accounted for in the report by Fajola and his associates). It is particularly meaningful in terms of the geographical distribution of Saprolegniaceae to note that the paper by Fajola *et al.* (1978) is one of the rare records of the recovery of species of *Saprolegnia* from the tropics.

DISTRIBUTION IN STREAMS (LOTIC WATERS)

Far less work has been done on the ecology of members of the Saprolegniaceae in rivers and streams than in lentic habitats. The bulk of the information on the ecological distribution of water molds in lotic waters comes from Suzuki's studies in Japan. While he analyzed polluted streams primarily (see section on pollution) he also studied unpolluted rivers as well (Suzuki, 1962d, 1964). In these latter bodies of water saprolegnians were very scarce or showed quite erratic patterns in distribution and frequency of occurrence (Suzuki and Tatsuno, 1964). There were no such inconsistencies in the study by Mil'ko and Belyakova (1968) of saprolegniaceous fungi in the Volga. They recovered specimens of these fungi more often from the water of the river (species of *Achlya*, and *Thraustotheca clavata*, for instance, were found only in the water) than from adjacent terrestrial habitats.

Kanouse (1925) contended -- presumably from qualitative observations rather than by actual counts -- that spores of *Achlya* and *Saprolegnia* species were so abundant in clear, rapidly moving water (brooks, rivers, lake shores) that other aquatic fungi could be nearly excluded. This general pronouncement has not been confirmed by later analyses, and it is without basis when individual species are considered. By way of examples, Stpiczynska's (1962) study of a peat bog region in Poland and our own unpublished investigations in Scandinavia may be cited. Stpiczynska found *Saprolegnia monoica*^t only in running water, but *Dictyuchus monosporus* and a species she identified as *S. ferax* occurred both in moving and stationary water. We have tallied the collecting data accompanying our recovery of watermolds in Iceland, Sweden, and Norway, and find that less than 18% of the isolates (3160 samples) came from mountain rivers and streams with rapidly moving water. We suspect that this low recovery percentage reflects a considerable dilution of propagative units rather than inability of the fungi to survive in such habitats. Sluggish streams (even very cold ones) in these northern countries are reasonably rich in watermolds (unpublished).

Farr and Paterson (1974) collected zoosporic fungi (including watermolds) from a polluted and nonpolluted stream in Virginia, taking soil samples from three points: channel sediments, the water's edge, and terrestrial locations removed from the stream margin. Only those samples from the channel bottom and from the water's edge yielded species of Saprolegniaceae, but there was no noticeable "preference" on the part of these fungi for either of these sites.

DISTRIBUTION IN WELLS

Achlya sp., *A. flagellata*^t, *Aphanomyces* sp., *Saprolegnia* sp., *S. monoica*^t, and *S. diclina* have been recovered from wells (Suzuki, 1961j). The frequency of isolation of watermolds from such a man-made habitat was consistently lower than the recovery of other microorganisms. Volz and Beneke (1972) isolated species of *Achlya* (nonsexual) from wells on a Bahamian island.

DISTRIBUTION IN RELATION TO POLLUTION

Pioneers in the collection and identification of members of the Saprolegniaceae held opposing views on the supposed occurrence of these fungi in polluted or stagnant waters. In time, studies were to show that watermolds did indeed occur in organic-enriched or industrial-polluted streams and sediments.

One of the earliest papers to report the recovery of a watermold -- *Saprolegnia* sp. -- from a polluted stream was that by J. W. H. Johnson (1911), and this was followed by Hamid's (1942) observation that saprolegniaceous fungi flourished in sewer water. Also among the early reports of these fungi in polluted water was that by J. V. Harvey (1952). He found that only representatives of *Aphanomyces* could be recovered from heavily fouled Ohio streams, but *Brevilegnia diclina* (among others) could be collected from those same watercourses following dilution by rain (the extent of sampling could well have influenced the results). By contrast -- and in some of the same streams sampled by Harvey -- W. B. Cooke and Bartsch (1959) found 15 species (members of *Achlya*, *Dictyuchus*, and *Saprolegnia*) in waters containing high levels of domestic and

industrial waste. While there was no correlation between pollution and occurrence, some aquatic fungi seemed not to grow well in "clean," natural bodies of water. Some collection data assembled by Kirgizbaeva (1976) indicate that some watermold species were very poorly represented in polluted bodies of water, yet could be recovered from biological filters used in wastewater treatment.

In 1956(a) and 1958, Höhnk published the results of a study of aquatic fungi along four watercourses subject to pollution. Although he collected many species of the Saprolegniaceae, he reported the distributional and abundance data on these fungi in terms of asexually versus sexually-reproducing forms. One lotic-lentic system that Höhnk (1956a) investigated was a stream draining into a series of small ponds thence through a forested area, and ultimately functioning as the effluent carrier for a dairy industry. Generally, there was a greater percentage of sexually-reproducing watermolds in the stream portion of the system than in the ponds, but at some sampling times the reverse was true. Watermolds appeared most often in samples taken at and near the source of the stream, were successively less abundant downstream toward the ponds, and were least frequent in that part of the aquatic system polluted by the dairy.

Rivers polluted by municipal wastes, Suzuki (1960g, h; 1961k, l) reported, harbored more watermolds downstream from the pollution sources than upstream from them. In every instance, the numbers of specimens of mucoraceous fungi and Deuteromycetes recovered from these streams far exceeded those of the Saprolegniaceae. None of the species of watermolds was an indicator of pollution in these Japanese rivers (Suzuki and Tatsuno, 1965a, b). Mil'ko and Belyakova (1968) obtained the greatest quantity of individuals of Saprolegniaceae (and the greatest diversity) from those sectors of the Volga River nearest populated areas, a result appearing also in a later study on the Volga by Mil'ko and Zakharova (1976). In connection with the abundance of saprolegnians in polluted waters, Willoughby and Collins (1966) discovered a significant feature. Propagules brought into aquatic systems via effluent may augment some components of the saprolegniaceous community already present in the system.

The Saprolegniaceae are not limited to streams carrying municipal or domestic wastes, but may be collected as well at sewage treatment sites. Haenseler *et al.* (1923) collected *Dictyuchus* sp. from stones in graded sprinkling filter beds, and found *Saprolegnia* sp. on exuviae of insects on those beds. The report by Rudolfs and Trajkovich (1924) of a nonsexual *Dictyuchus* in an identical habitat is of interest. Their observations suggest that this particular watermold was not a mere transient visitor to the filters. Moreover, the population of *Dictyuchus* sp. appeared to fluctuate in response to the peak occurrence of a *Penicillium*. When the *Penicillium* species reached its maximum frequency on the filter stones, specimens of the *Dictyuchus* became more abundant. By plating water samples, J. G. Becker and Shaw (1955) recovered members (unidentified) of *Saprolegnia* and *Isoachlya*† from the effluent of primary and secondary settling tanks and primary filters.

The most extensive studies of watermolds in sewage treatment systems are those by W. B. Cooke and Matsuura (1969), and Logvinenko (1970). The former investigators isolated species (but did not identify most of them) from several locations at a waste stabilization pond and adjacent areas: raw sewage, sludge (influent and effluent pipes), pond scum and pond water (receiving sewage), and water above and below the outfall.

Representatives of the family were also collected from undisturbed soil in the area. The number and diversity of species was not great, but viable propagules clearly existed in wastewater with an extremely high BOD. Logvinenko (1970) found water molds in five processing stages of a waste treatment plant (influent, initial and second treatment, biological filtration, and effluent). Not one species of *Achlya* occurred in the wastewater; this is in agreement with the report by Hasija and Batra (1978) who collected *A. americana* only in unpolluted waters. Members of the genus *Saprolegnia* are evidently sometimes as abundant in sewage water courses or on filters as is *Leptomitius lacteus* (Wurtz, 1956), and W. B. Cooke (1969) has isolated *Achlya klebsiana*[†], *Brevilegnia diclina*, and *Thraustotheca clavata* from soil flooded with sewage sludge.

Water molds are also found in aquatic habitats polluted by industrial wastes. Suzuki and his associates (1960) established a series of stations along a 350 meter section of a river receiving sugar refinery wastes. A nonsexual *Saprolegnia* occurred abundantly above and below the outfall, but was also isolated from water at the effluent site itself. An unidentified *Achlya* and *Aphanomyces* sp. were sparse in the refinery-polluted river system, and for all practical purposes did not occur in the organic-rich portion of the stream. Wurtz (1956) also reported species (unidentified) of *Saprolegnia* in streams polluted by waste from food and sugar processing plants. Water molds could not be isolated directly from the effluent of an industrial plant manufacturing alcohol, Suzuki *et al.* (1961) reported, but such fungi were found upstream and downstream from the outfall. Some data published by Suzuki (1960d, 1962c) on the occurrence of saprolegnians in waters carrying industrial pollution are to a degree contradictory. He reported that industrial wastes restricted the occurrence of species, yet the maximum number of isolates of saprolegniaceous fungi came from those portions of streams where such wastes were most concentrated (Suzuki, 1962c). It should be emphasized that water molds were not the dominant fungi in these streams.

Only a few other reports of saprotrophic water molds in relation to industrial pollution exist. Stjerna-Pooth (1957) found that *Achlya prolifera* was the dominant zoosporic species in wastewater from the manufacture of wood fiber wallboard. The fungal flora of streams transporting radon runoff has been compared (Mil'ko and Dudka, 1968) with streams not so polluted in this fashion. While their abundance was low, four species -- *A. racemosa*, *Aphanomyces laevis*, *S. delica*[†] and *S. ferax* -- were isolated from the radon-polluted water. Farr and Paterson (1974) collected water molds from sites at, above, and below the outfall from an industrial plant. There were more species of Saprolegniaceae in the enriched water than in the unpolluted regions, but there were fewer species at the outfall site proper than at other points in the stream. Streams carrying acid mine drainage from soft coal regions harbor viable propagative units of species (unidentified) of *Achlya*, *Aphanomyces*, *Dictyuchus* and *Saprolegnia* (W. B. Cooke, 1976a).

Some remarks by Peduzzi (1973) and Wurtz (1956) relate pollution in a general way to the activity of *Saprolegnia parasitica*, and other species associated with fish (Chapter 29). Wurtz (1956) believed that *S. parasitica*[†] assumed a saprotrophic existence when inhabiting polluted waters but was otherwise parasitic. Eutrophication -- the augmentation of organic matter in water -- Peduzzi (1973) thought, was favorable to the saprotrophic "phase" of water molds that can invade fish. On the other hand, pollution

was unfavorable to this phase of the fungus at the level of the fish epidermis, and spores (by means of germ tubes) provided for the fungus a route to a parasitic existence.

The various published reports of members of the Saprolegniaceae in polluted waters leave no doubt that some species can tolerate such unfavorable habitats. However, survival or mere existence there does not grant these fungi an autochthonous status. Is it possible, even though experimental evidence is not at hand (so far as we are aware), to categorize the water molds in relation to pollution (or lack thereof)? Wurtz (1957) has provided some insight into this question by recognizing six "zones of saprophytism" based upon the degree of purity of the water. He regarded members of *Saprolegnia* (species?) as occupants of two of these zones, the polysaprobe one (consisting of strongly polluted, oxygen-deficient water with intense decomposition and production of "fermentative gas"), and a somewhat less polluted area, the α -mesosaprobe zone. The waters of the latter zone are polluted, accumulate the organic acids that accompany decomposition, and contain in addition some oxygen, sugars, and amino acids. A partial answer to the foregoing question appears also in the categories of organisms with respect to their occurrence in polluted habitats recognized and named by W. B. Cooke (1957). No saprolegniaceous fungus could be classified as lymbiontic because none grew only in the presence of pollutants. Perhaps a few water molds might be recognized as lymaxenous species (under certain circumstances, or as chance invaders), but the existing ecological distributional evidence points to the majority of these fungi belonging to the category of lymaphobus (W. B. Cooke, 1957) organisms.

DISTRIBUTION IN TERRESTRIAL HABITATS

Following J. V. Harvey's (1925a, b; 1927b, c) demonstration that some species of Saprolegniaceae were more common in terrestrial than aquatic habitats collectors turned their attention to isolating these fungi from soil. Cook and Morgan (1934: 348) did considerable collecting utilizing Harvey's methods, and concluded that members of the family as a group were primarily terrestrial. Some species, they maintained, adapted (phenotypically? genetically?) to a completely aquatic existence that, as in the case of *Saprolegnia parasitica*[†], culminated in "... total parasitism..." They were also the first to suggest that the occurrence of water molds was periodic and their ecological distribution in soil appeared to be influenced by locality (relatively dry versus relatively wet sites). Wolf (1939b) concluded that species of *Brevilegnia*, presumed to be limited to soil (which they are not, as our studies in Iceland show), displayed a notable lack of endemism.

Other investigators have also commented (in a geographical frame of reference) on ecological aspects of the occurrence of water molds in soil. For example, Harder and Gallwitz-Uebelmesser (1959) simply reported that about 55% of the family. Yung and Stenton (1964), on the other hand, could demonstrate no real differences in the ecological distribution of Saprolegniaceae in relation to the sampling site in the Hong Kong region (wooded slopes versus paddy rice fields). The collections by Apinis (1958) of water molds from alluvial soils of England seemingly were too sparse to permit him to draw any conclusion of ecological significance, but in later work he was able to relate distribution of these fungi to plant community types.

DISTRIBUTION IN QUADRAT-DEFINED SOILS

Emerging from the pioneering efforts of Dick (1962, 1963, 1966, 1968a) and Dick and Newby (1961) is a wealth of information on the occurrence of water molds in samples taken in reference to area restrictions imposed by quadrat methodology. From the very extensive data reported in these accounts patterns of seasonal occurrence (see Chapter 5) can be detected. The foremost contribution of these papers, however, is not to be found in the ecological distributional patterns uncovered for individual species. Rather, the work by Dick and Newby provides insight into principles of what we shall call common sense ecology that, if ignored, lead to equivocal data. Their accounts comprise more than descriptive ecology, and thus demand close attention. The following paragraphs are a harvest of the chief elements from these and papers of a like nature. In soil there are aggregate patterns of distribution (Dick, 1962; 1976: fig. 20.2; Prabhuji, 1979) for some species of Saprolegniaceae such that they are clustered in particular regions of small sectors of soil rather than being uniformly distributed in a given area. Even over distances of a few centimeters, the data (Dick, 1962) show, the composition of the water mold mycoflora in soil varies noticeably. Presumably, the restricted nature of ecological distribution in soil of individual species -- their tendency to occur in population centers, as it were -- is formulated in part by the extent of planont or encysted spore dispersal.

Little is known of spore movement as it relates to the soil-habiting saprolegnians, but some studies on infection of pea roots (*Pisum sativum* L.) by *Aphanomyces euteiches* provide some clues. Although spores of *A. euteiches* evidently remain viable (and virulent) in soil up to seven days (Haenseler, 1925), they likely travel as planonts less than 1/2 inch (13 mm) unless aided by free water movement (Haenseler, 1925; Hickman and Ho, 1966). Experiments by J. L. Lockwood and Ballard (1959) yielded the highest incidences of root rot in pea seedlings when spore inoculum was placed as close as possible to the susceptible tissue (they tested planont movement over distances of 1-5 cm).

It is well-established that the ecological distribution of a species is a response to multiple biotic and abiotic environmental factors. Dick (1963) showed, for example, that some species (in quadrat sampling) were characteristic of wet soils of low pH (*Saprolegnia asterophora*, *S. litoralis*, and *S. turfosa*, for instance). Others *Aplanopsis terrestris* and *Aplanopsis spinosa*[†] most frequently occupied drier soils having a wide range of pH.

Species distribution (in the ecological, not geographical sense) is independent of their assignment to genus (Dick, 1963). Höhnk's (1935a) grouping of genera into five "sporulation types" (see later section) fails at points when individual species are taken into consideration. *Pythiopsis cymosa* and *Saprolegnia megasperma*, to name two examples, occur in dry as well as wet soil sites (Dick, 1963), but if Höhnk's theory is correct they would be expected to appear only in wet areas.

Observations suggest that there can be a relatively constant flora of water molds in any given soil site, yet still be apparent seasonal fluctuations in the frequency of appearance (on culturing) of the individual species making up the composite population (Dick and Newby, 1961). Correlations in patterns of species distribution or

occurrence among sites may appear to be low or nonexistent if sampling is random and not repetitive. Readily recognizable patterns may emerge, however, if samples are taken repeatedly from quadrat-delimited areas. A correlation also appears to exist (Dick, 1966) between distribution patterns of individual species and site topography. Some species seemed to be restricted to higher ground, others to low-lying regions, and still others appeared to be distributed without regard to the slope.

The assay of soil for spore abundance is not a valid measure of the frequency or activity of the Saprolegniaceae in that habitat (Dick, 1968a). Representatives of *Aplanopsis*, Dick (1966) found, were more frequent in soil -- even though they seem not to produce sporangia -- than some water molds that do reproduce asexually.

DISTRIBUTION AT TERRESTRIAL/AQUATIC INTERFACES

It would be expected that if differences existed among water molds in ecological distribution patterns and frequency the disparities would appear most readily in areas where two ecotones adjoin. The few studies of such a pair of systems -- at a soil/water interface -- show that differences do exist, if not with respect to individual species of water molds, at least on a population frequency basis. Klich (1980) presented data to suggest that species of *Achlya* and *Dictyuchus* are more common in water subject to leaching effects from the soil than in other habitats. This appears to confirm studies by Willoughby (1962) and V. G. Collins and Willoughby (1962). Species of *Saprolegnia* and *Achlya*, Klich found, however, were most commonly recovered from water where there was little possibility of substantial inflow from leaching. Work by O'Sullivan (1965), and Dick (1966, 1968a, 1971c) are prominent in this regard. Overman's (1970) investigation of three habitat zones in an impoundment area was quite brief, and the results indicated that there were fewer water molds in the flood area (periodically inundated marginal soil) than in the unflooded areas or in submerged sediments.

O'Sullivan (1965) sampled along transects (of given linear distances) marking a gradient of sites from strictly exposed to continually submerged ones. From an analysis of the data she proposed that there were six recognizable but rather narrow categories of species each delimited in relation to the percentage of the total number of isolates secured. The groupings were:

- I. aquatic: collected only from water -- 4%;
- II. aquatic and damp terrestrial: isolated from water and closely adjacent soil -- 16%;
- III. aquatic and general terrestrial: found in water and adjacent soil from the water's edge to the maximum transect distance upland -- 20%;
- IV. damp terrestrial: species found in the soil only, but near the water's edge -- 28%;
- V. terrestrial: occurring only in soil but not at the maximum distance from the water line -- 24%;
- VI. distant terrestrial: collected only in soil and then exclusively at distant upland points -- 8%.

With increasing distances from the waterline there were both fewer species and fewer individuals recovered from the samples. Some species such as *Achlya flagellata* and *A. racemosa* were at their maximum frequency at the waterline; others -- *Pythiopsis cymosa* and *Thraustotheca clavata*, for instance -- were collected most frequently at some distance from the water margin. *Aplanopsis spinosa*^t, notably, was widely distributed in both wet and dry soils (Dick, 1966, isolated this species least frequently in waterlogged soils). As O'Sullivan pointed out, her data suggest that Höhnk's (1935a) generic groupings as to sporulation type and habitat oversimplified what is likely a very complex series of distribution patterns. *Pythiopsis cymosa*, for example, should inhabit the aquatic environment because it consistently produces only motile spores, but O'Sullivan isolated the species most frequently from soil.

From a selection of four categories of sites -- seldom or never inundated, poorly drained, subject to flooding, and permanently waterlogged -- Dick (1966) isolated and identified 32 species of Saprolegniaceae. The wetter sites harbored the greatest diversity of species. Moreover, there was no pattern of "distribution of genera" (Höhnk, 1935a) among the soils because of the wide variations in occurrence of individual species with respect to the site. Shipman (1977, 1979) compared the species composition at various sampling sites by applying to her data Sorensen's Index of Similarity. The resulting numerical index in fact showed site differences with respect to composition of the watermold populations, as did chi square testing applied to members of the Saprolegniales versus the Pythiales in seven habitats. Both in creek sediments and water, representatives of the former order outnumbered significantly those of the latter.

The results of a thorough study of relative abundance and ecological distribution of Saprolegniaceae in submerged and emergent sites was published by Dick in 1971(c). He sampled (without repetition) 67 shoreline and sediment sites, and also sought fungi in samplings made along five transects. Three transects crossed the study site lake such that samples could be taken from sediments. When the results of recoveries from the sediments were analyzed there were no evident trends in species distribution. Moreover, the data indicated that the depth of water above the sediments did not influence the distribution of individuals "associated" with the bottom deposits. The muds subtending lentic waters of the lake were poor both in species diversity and abundance of individual propagules. Generalizing from the data from single-sampled sites, Dick recognized three clusters of species making up the populations of watermolds at the submerged sites. One was the *Achlya racemosa* group including some members of *Saprolegnia* but very few species with eccentric oospores. The *Achlya apiculata* group, on the other hand, was comprised largely of individuals with eccentric oospores, but with a few species of *Saprolegnia* and others (including *A. apiculata* itself) with centric oospores. Nonsexual Achlyas were dominant in a third group. Dick also found a sharp difference in the relative abundance of propagules from samples of sediment at the waterline compared with those in samples of bottom material submerged at one meter and beyond. Many more samples that did not yield watermolds were taken from the latter sites.

Dick (1971c:337) concluded that the Saprolegniaceae as a group are best thought of as fungi characteristic of the emergent littoral zone (centered at the water line) and

the lentic/littoral zone. Very few species were singled out as characteristic residents of the lentic regions of the lake he sampled. As is evident from Figure 3 (adapted from Dick, 1976; see Fig. 20.6 in this publication for percentage correlations between sites) the maximum number of species occurred in the littoral zone samples. Correspondingly, the fewest number of samples failed to yield water molds on culture (percentage of the total of 80 samples at each site; the limited sampling in a short span of time may not reflect meaningful percentages of correlation). From samples taken farther from the shoreline, toward the deeper waters, the number of species isolated decreased and concomitantly the number of negative samples increased.

Based on several incidental observations made during his studies Dick (1968a) proposed a scheme that (1) predicted possible propagule movements from terrestrial to aquatic sites across the littoral zone (margin of soil and water line), and (2) called attention to morphological differences among the resident water molds in these three general habitats (Fig. 4). According to Dick, the resident water molds in soil tend to have slender hyphae (less "demand" for water, he suggested) and are likely to produce a resistant stage (oospore?) more readily than planonts. The wide geographical and ecological distribution and frequency of *Aplanopsis spinosa*[†] in soils (Dick, 1963, 1966) would certainly account for his prediction that individuals with small, ornamented oogonia frequent terrestrial zones (at lake margins), and give way in wet habitats to ones with large, smooth oogonia (we have analyzed our collection data of more than 3000 isolates largely from the Scandinavian countries, but cannot confirm Dick's hypothesis). The trend in propagule movement is from land to water (Fig. 4), with the natural rise and fall of the water level serving to transport propagative units to some degree toward rather than away from land. Of course, retention of resident members (indwellers; Park, 1972b) of the soil community would be possible only if the individuals were capable of growth and reproduction sufficiently persistent to ensure that they would not be eventually depleted from the soil. If Dick's (1968a) predictive scheme in fact operates in nature, migrants and versatiles (Park, 1972b) become essential elements of communities of water molds.

DISTRIBUTION RELATIVE TO COMMUNITY AND HABITAT TYPES

We have in previous sections referred to the groupings of genera by sporulation type, as proposed by Höhnk in 1935(a). He developed the scheme by correlating isolations of members of the Saprolegniaceae with five habitat types that he sampled: I, tidal water (Weser River Basin between Bremerhaven and Bremer, West Germany); II, river and adjacent stream water; III, ditch water; IV, soil from the river shoreline, and V, soil from fields bordering the river. The five groupings of genera whose representatives appeared predominantly in each habitat type I -- *Pythiopsis*; II -- *Saprolegnia*, *Isoachlya*[†], *Leptolegnia*; III -- *Achlya*, *Aphanomyces*, *Plectospora*; IV -- *Thraustotheca*, *Calyptralegnia*, *Brevilegnia*, and V -- *Aplanes* and *Geolegnia*. Höhnk noted that within these groupings of genera the species have a common denominator in spore release and behavior patterns (for example, the discharge of immediately motile spores by members of groups I and II). The pertinent data from his account are summarized in Table 16 showing the percent occurrence (his term) of isolates of a particular sporulation type in relation to

habitat type. Individuals with *Saprolegnia*-type spore release (II) predominated in water, but in soils, those characterized by a nonmotile primary spore stage (IV) or having no motile spores at all (V) were the most frequent.

Höhnk (1935a) concluded that there was an adaptive (phenotypic?) progression of sporulation types (by water molds) from aquatic habitats to terrestrial ones. Later he (Höhnk, 1968) was to expand this concept somewhat to indicate that populations of Saprolegniaceae, residing in the transition from aquatic to terrestrial habitats, changed also with respect to predominant oospore number and preponderance of parthenospory (Fig. 5). Höhnk's theory has not enjoyed full support from later studies, and appears not to represent a general situation in the ecological distribution of water molds. One of the chief objections to his concept is that many of the representatives of the genera forming the basis for the five groups have multiple patterns of spore release, and individuals might well "shift" to alternate methods in particular habitats or under particular environmental stresses. Dick (1968a) found that species of water molds with multiple oospores occurred frequently in constantly wet or submerged habitats, and gave way in predominance in terrestrial situations to ones with single oospores (Fig. 5).

Other studies of the ecological distribution and abundance of water molds patterned after that of Höhnk (1935a) have appeared from time to time. There is, however, an unfortunate common denominator among these investigations, namely, that the results are given in terms of the occurrence of genera. It hardly needs emphasizing that genera are not distributed (their representatives are) but this is not the basic blemish in these studies. Data reporting the distribution of genera tell nothing of species frequency or density; hence it is impossible to say whether those genera were represented by broad species diversity or only by one or a few dominant forms. We therefore limit our consideration of these accounts to their more general conclusions.

Gaertner (1954) studied the occurrence and abundance of keratinophilic Saprolegniaceae (among other fungi) in soils from a variety of habitats in Africa, Sweden, and Middle Europe: savannah, bush, riverbanks, gardens, parks, roadways, and the like. In general, he found that the keratinophilic water molds made up less than 10% of the total fungal population uncovered in the various regions and habitats sampled. The highest yields came from soil in roadside ditches. *In toto*, Gaertner's data suggest that there were fewer water molds in northerly latitudes than in southerly and equatorial regions, but much confirmatory evidence is needed. Harder (1948) also reported the percentage of occurrence of genera in nine habitat types in Germany. Members of *Saprolegnia* and *Aphanomyces* predominated overall, with their greatest frequencies in shoreline soils and in those from ditches and pastures. The work of Remy (1950) differed little in its conception and procedures from that of Harder. She also sampled soils in a variety of habitats (such as gardens, pastures, forests, and meadows), and tallied results as "frequency of genera isolated." Remy's data indicate only that (1) species of *Aphanomyces* were most frequent in the majority of habitats sampled, and those of *Dictyuchus* occurred least regularly and in the fewest habitats; (2) there was a greater diversity of species recovered from loam soils than from sandy ones. It may at least be said that Remy's study confirmed Niethammer's (1937) contention that species of *Aphanomyces* predominated in soils. Certainly we have found this latter

situation to be true of soils of northerly latitudes (Scandinavian countries) but hardly the case in tropical regions that we have investigated.

None of the studies just mentioned exceeds in diversity of habitats sampled those published by Sörgel (1941) and A. Lund (1978). Sörgel isolated water molds -- but identified them only to genus -- from soils of forests, pastures, caves, gardens, xerophytic shrub zones, ocean shorelines, rain gutters, old wells, and roadside ditches (among other habitats) in the West Indies. Members of the family were more frequent in soil samples from forests, cultivated lands, and stream banks than from any other sites. As to representatives of genera, these facts emerge from his study: (1) species of *Achlya* were isolated from more soil samples than were individuals of other genera; (2) the fewest fungi recovered were members of *Brevilegnia*, *Aphanomyces*, *Pythiopsis*, *Leptolegnia*, *Thraustotheca*, *Geolegnia* and *Aplanest*; (3) not one sample yielded species of *Saprolegnia*; (4) members of *Achlya* and *Dictyuchus* were found more frequently in wet than in dry soils. On the whole, Sörgel collected more fungi -- including water molds -- in man-modified habitats or those in the vicinity of standing water than in any other sites sampled. Dick's (1968a) analysis is not at variance with Sörgel's data: the variety and abundance of water molds is greatest in wet soils and in mud and soil adjacent to free water.

Like Sörgel, A. Lund (1978) sampled a wide variety of cultivated and uncultivated habitats for water molds. He collected in uncultivated soils near ponds and bogs, from a beech forest and a spruce plantation, and from a grassy field; cultivated soil samples came from fields of grass or grain near ponds and lakes, from gardens and parks (also near bodies of water) and from planted fields not adjacent to water. He divided the species recovered into two groups: A, those known to occur both in freshwater and soil, and B, those found principally if not exclusively in soil (representatives of *Thraustotheca*, *Brevilegnia*, *Geolegnia*, and *Aplanopsis*). The majority of water molds collected from soils in the vicinity of bodies of water were in group A; members of group B were most abundant in moist, cultivated soils. Not surprisingly -- since he was sampling terrestrial habitats -- Lund found about three-fourths (72%) of all the water molds isolated to be in group B.

Three investigators, Apinis (1960, 1964), Logvinenko (1971), and Nesom (1969), have attempted to relate the ecological distribution of Saprolegniaceae to vascular plant community types. The work of the former is the most generous in terms of scope and results.

Apinis (1960, 1964) analyzed the flora of zoosporic fungi (including the Saprolegniaceae) in ten communities: two pasture types (*Lolio-Cynosura*, and *Ranunculus repens-Alopecurus*), two marsh types (*Agrostis* and *Glyceria*), two swamps (floating *Glyceria* species in one, *Scirpus-Phragmites* predominating in the second), and four zones in the initial stages of marsh development (no vegetation, *Glyceria* communities, *Phragmites* stands, and *Salicis* zones). He determined both the occurrence (number of isolates/number of samples x 100) and percent frequency. The most frequent (occurring in at least three habitat types) and widely distributed species were *Achlya racemosa*, *A. spinosa*, *Achlya* sp., *Aphanomyces scaber*, *Brevilegnia unisporma*, *Dictyuchus monosporus*, *D. pseudodictyon*, *Saprolegnia* sp., and *S. ferax*. The least abundant forms were *A. apiculata*, *A. colorata*, *A. imperfecta*[†], *A. polyandra*, *A. radiosa*, *Isoachlya*[†]

anisospora, *I. unispora*[†], and *Thraustotheca clavata*, and these were also very much restricted in their ecological distribution.

In general, the data from Apinis' study (1960, 1964) point to a predominance of watermolds in specific communities, namely, *Ranunculus-Alopecurus* (pasture land), the marsh communities of *Agrostis* and *Glyceria*, and the *Glyceria* community of swamps. Certain species appeared to have a "preference" for certain habitats dominated by particular vascular plants. *Achlya apiculata* was a common inhabitant of marshes and waterlogged pastures, but *Brevilegnia unisperma* "preferred" waterlogged and dry pastures. *Dictyuchus monosporus*, *Saprolegnia ferax*, and *S. glomerata* were most frequent in marshes and swamps, while *A. spinosa* was in effect "indifferent" to habitat type. Within limits, only a few species of Saprolegniaceae could be viewed as part of a particular vascular plant community: (1) *A. radiosa* limited to the community predominated by *Ranunculus* and *Alopecurus*; (2) *A. colorata*, *A. imperfecta*[†], and *A. polyandra*[†] Hildebrand associated only with the "terrestrial" marsh zone populated by *Glyceria*, and (3) *Isoachlya anisospora*[†] exclusively limited to the *Scirpus-Phragmites* zones in swamp communities. Save for *S. ferax*, Apinis isolated very few watermolds from the early successional communities leading to marshes.

Nesom's (1969) study on distribution and abundance of zoosporic fungi -- only two watermolds were collected, *Achlya klebsiana*[†] and *Leptolegnia* sp. -- centered in a soil filled depression or "island" community in a granite outcropping. She did not attempt to relate the species to the phanerogamic segments of the community but did consider organic content of the soil as a major parameter for analysis. Where the organic deposition from the vascular plants was in the range of 4-6%, watermolds could be isolated.

An uneven distribution of watermolds (and other zoosporic fungi) in a river in the Carpathians was uncovered by Logvinenko (1971). The ecological data in his paper are brief, but in essence point to fewer saprolegniaceous species in the montane reaches of the river than in its sectors at low elevations. He attributed this pattern to the scanty emergent and submerged "macrophytes" in and bordering the river in its mountain course, and an abundance of such vegetation in it at the lower elevations.

Klich (1980) related watermold composition to general site characteristics of an aquatic habitat. *Aphanomyces laevis* apparently was restricted to aquatic sites in or near emergent vegetation, while *Saprolegnia diclina* was isolated most frequently from water samples collected in sand/gravel bottoms with no rooted aquatic vegetation. None of the species recovered by Klich was restricted to a lotic habitat.