

CHAPTER 5. Ecology: Seasonal Occurrence

In the pursuit of watermolds investigators have discovered what has been interpreted as a kind of seasonal periodicity: species appearing more or less frequently in samples taken in some months but not in others. The cases of seasonal appearance that have been uncovered suggest that some representatives of the family are permanent residents of a site, while others are transients or only sporadic invaders. As interesting as the study of the phenology of the Saprolegniaceae might be, it is a demanding task, for the gathering of data must be based on thorough, precise methodology, and the results must be interpreted very cautiously.

Seasonal periodicity calls to mind the fluctuations of temperature, light, water, nutrients, and the like, attending the annual sequence of months. Inexplicably, most of the published information either shows phenology of watermolds in relation to the months of the year in which particular species predominated or appeared, or in terms of the usual four seasons. Investigators reporting such observations appear to assume, for example, that the temperature fluctuations commonly associated with seasonal changes are universally known. Temperature changes with season may be less important, however, than concomitant physico-chemical variations in the particular habitat. In the tropics the observed seasonal changes in the occurrence of watermolds might be interpreted to indicate an association with rainfall (Alabi, 1971a, b) but certainly not with temperature. In any case, the inhabitants of a community may be sporadic not because of the season of the year but because of fluctuations in soil moisture or amounts and duration of run-off. They may seem to be periodic in occurrence because they are closely interrelated with (if not dependent upon) such predictable seasonal events as leaf fall, insect metamorphosis, or local applications of organic or mineral fertilizers.

The causal factor behind evident seasonal fluctuations, then, are not easy to define; often they are simply not even mentioned by investigators. Moreover, it must be confessed that some accounts of the phenology of the watermolds carry with them little restraint on the temptation to generalize. Attempts to interpret or to compare and contrast the various existing reports on periodicity are at once frustrated by limitations arising from disparate amounts of sampling, lack of statistical data, and a variety of other impediments. In reporting seasonal occurrence, some investigators have grouped species in violation of sound taxonomic principles, while others have simply recorded specimens as unnamed taxa. Some accounts are based on isolations of Saprolegniaceae from water, others from soil, and still others from samples of both soil and water. "Seasons," moreover, may be listed as warm or cold, wet or dry, winter or summer, or just months of the year. Most reports do not mention the latitude of the sampling sites, although there is more than just a little difference in duration and intensity of environmental gradients between winter in Florida and in Poland.

The following account of the published record on seasonal periodicity in the Saprolegniaceae is necessarily generalized, and conclusions drawn from the information in this chapter may well be open to considerable error. We attempt to single out coherence among the various reports that authors have assumed will support

the reality of phenology in this family, but at the same time we call attention to inconsistencies. In the final analysis, it will be obvious that the whole subject of seasonal occurrence of Saprolegniaceae has been approached with scant attention the methodology, essentially no statistical analyses of data, and almost no recognition of specific environmental characteristics that circumscribe seasons. Nevertheless, these serious shortcomings must not rule out an account of research that has been done.

GENERAL TRENDS IN PERIODICITY

If one wishes merely to note whether there are apparent seasonal fluctuations in the occurrence of the Saprolegniaceae, a host of taxonomic papers carry that information: Apinis (1929a, b), Bock (1956), Bretsnyder (1943), Chaudhuri *et al.* (1947), Florinskaya (1969), T. W. Johnson (1956a), A. Lund (1934), Milovtsova (1935a), Naumov (1954), Peterson (1909a, 1910), Scott (1960a), Waterhouse (1942), and A. W. Ziegler (1952). These accounts do not necessarily entertain the same conclusions reached by longer, ecologically oriented ones. A broad scanning of some papers dealing with the periodicity of Saprolegniaceae will illustrate the breadth of work that has been done. It should be borne in mind that studies on annual fluctuations probably should be carried out for no less than 18 months. Ideally, work of this nature should be conducted for five years or so, although only one seasonal investigation has to this point gathered data over such a time span (Logvinenko and Meshcheryakova, 1971).

Bretsnyder (1943) reported that species in the family were in greatest abundance in cold water, and decreased in frequency as the water temperature rose; her study, however, was only three months long. From an investigation of equally short duration, Schmitt (1967) reached essentially the same conclusion. He recovered more members of the Saprolegniaceae in the sampling site (Lake Texoma, Oklahoma) during early summer (cool) than in the late summer. Isolations from a series of Indian ponds led Dayal and Thakur Ji (1969) to predict a summer dormant season for the water molds, with a peak of abundance in March, and a low point in October. Nine species of water molds collected by Dayal and Tandon (1962), also in Indian ponds, appeared most frequently in the fall and winter samplings. They suggested that oospores were the source of inoculum, and that these cells were dormant during the summer months. Mer and his associates (1980) found minimum numbers of species in water in winter, spring, and autumn, but in soil, the minima occurred only in the winter months. Some South African water molds, Goldie Smith (1948) found, were most abundant in the spring during the dry season of this region. Other very brief and decidedly limited accounts of periodicity in occurrence of water molds appear in the following publications: Florinskaya [1969 – listed four species, only one of which, *Saprolegnia parasitica*[†] was found throughout the year (as an invader of fish in rearing ponds)]; Hamid (1942) reported that favorable times for the development of water molds were in February to May, a period corresponding to a rise in water temperature); Ho (1975c) noted that the maximum isolation percentages for *Achlya* and *Saprolegnia* species were attained in spring and autumn samplings; minimum percentages occurred in the summer and

winter); Milovtsova (1935a, reported the richest yield of water molds in samples collected in June and July, but with *Achlya* species predominating in autumn collections, and members of *Saprolegnia* being most common in samples taken in the spring); Muhsin (1977, isolated and identified 20 species of water molds in river waters in Iraq, finding January to be the peak month for frequency and diversity of species, but with the lowest frequency occurring in the summer and early autumn); Ramsbottom [1931, stated that the best "season" for collecting aquatic fungi (including water molds) in England, was spring through autumn (November)]; Overman (1970, suggested that there were two periods when water molds were most frequent in an Illinois river system, namely, summer because of its high temperatures and autumn when there was a substantial influx of organic matter suitable for nutrient substrates.

It is to be emphasized that interpretation of an apparent seasonal periodicity of water molds must be based on very careful attention to methodology. For example, Ismail *et al.* (1979) concluded that their field collection data pointed to seasonal rhythmicity with respect to the occurrence of species of *Saprolegnia*. They found no species in the summer when water temperatures were above 28 °C, but did recover representatives of the genus from samples collected when the water was colder than 16 °C. In the laboratory, however, all samples were incubated at 22 °C when baited, and the recovery of species was thus predicated on a single temperature. The study by Rattan and his associates (1979) on the occurrence of specimens of *Dictyuchus* and *Calyptralegnia* shows a similar restriction imposed by methodology.

As a reflection of environmental differences associated with particular geographical regions, noticeable disparities have appeared in the tabulation of seasonal abundance of water molds in general (Table 17; this table does not take into account such variables as length of study or database). Chaudhuri *et al.* (1947) found two seasons favorable for increases in numbers of water molds, an autumn period prior to onset of cold weather, and an early spring season marked by a warming trend. Maximum yields of species, Dick and Newby (1961) reported, came from soil samples collected in the spring and autumn (in southwestern England), but according to Hunter (1975) many of the species of Saprolegniaceae she collected (vicinity of Cambridge, England) were more common in the winter (December and January) than in early spring (February and March). However, there was a gradual increase in frequency from the low spring yield to a peak in the summer. The greatest variety of species gathered by Maestres (1977) in a Newfoundland river appeared in March, July, September, and November, with the least diversity occurring in samples collected in December and January. Counts of water mold propagules displayed a decrease from March through September.

The data on periodicity assembled by R. E. Roberts (1963) showed a low frequency of isolates and a narrow spectrum of species (in English waters) during warm seasons, an increase in water molds in autumn, and a maximum number being recovered in the spring. These data are in agreement in large part with the earlier findings by Forbes (1935b) and to some extent with those of Perrott (1960). The latter included periodicity data only for *Achlya colorata*, *A. radiosa*, and *Dictyuchus sterile*^t,

listing them as winter and spring species. If, by "...peak of activity..." Forbes (1935b: 5) meant abundance or frequency, then members of the *A. prolifera* galaxy of species were noticeable "winter-favoring" fungi.

In contrast to the trends of watermold occurrence appearing in British waters is the report by Rooney and McKnight (1972) of some collections of saprolegnians in a Utah lake. They found the number and frequency of these fungi to increase with the seasonal rise in water temperature beginning with the onset of the ice-free period in May. Stpiczyńska-Tober's (1965) records of Saprolegniaceae from two rivers in Poland are extensive. They show the greatest frequency of specimens and diversity to come from the rivers when the water was 5-18 °C. She found more representatives of the family in samples from water at -2 to -5 °C than in those taken when the temperature was 18-30 °C. Although Mil'ko's (1965) data are scanty they do indicate that watermolds are in general more frequently found in the Danube delta region in the summer than at any other time of the year even though species diversity is least in the river water itself. In any case, the contrast in the observations by Stpiczyńska-Tober and Mil'ko is striking.

It is doubtful that TeStrake's (1958) data on distribution of Saprolegniaceae demonstrate seasonal periodicity of individual species because fluctuating salinity was a major hydrographic factor in the North Carolina estuary which she sampled. If possible salinity influences are ignored, it is apparent that *Achlya flagellata*† and *A. prolifera* would qualify as "winter" species (most abundant in the estuary water at 4.5 - 5.5 °C) while *A. americana* could be classified as a "summer" occupant of the stream (May, June; water temperatures of 20-26 °C). Furthermore, if TeStrake's data are analyzed on the basis of oospore type, the fungi she collected display a seasonal periodicity.

Suzuki's studies on Japanese lakes and rivers included field site sampling to determine seasonal variations in the populations of Saprolegniaceae. The patterns of periodicity that he reported were based on his estimate of the number of planonts produced by relatively few representatives. In some aquatic habitats species of *Saprolegnia*, *Dictyuchus* sp. and *Isoachlya eccentrica*† (Suzuki, 1960b, c, f) occurred principally in the months when colder waters prevailed (winter and early spring) while *Achlyas* appeared most often in water samples harvested in the summer months. Members of *Aphanomyces*, on the contrary, were recovered throughout the year, although, to be sure, there were peaks of frequency.

If the data on watermolds occurrence in two or more Japanese lakes are compared on an individual species basis, there is prominent variation in some cases as to months or seasons during which particular species predominated. Suzuki (1960c) believed that the effect of water temperature on saprolegniaceous fungi was expressed largely in spore production, but that "periphytic" bacteria also influenced sporulation by the resident watermolds. He reported in 1960(f) that there were salient periods of maximum frequency of spores of all species of saprolegnians in one Japanese pond - a maximum in the spring and another in autumn. There were two periods, summer and winter, when spore frequency was at its lowest. These observations, however, are not

in full accord with the graphic data included in this account. In 1961 Suzuki and Hatakeyama reported a periodicity of watermold spores in a Japanese lake during the months of August to November of one year. The calculated number of spores (by month) appears to be extremely low (when compared, for instance, to counts which Willoughby, 1965, recorded). In early August, the spore count was <100 cells 10 mL^{-1} ; from mid-August to mid-September the number increased to >500 10 mL^{-1} , then fell, between mid-October and the end of November, to a level of <50 10 mL^{-1} . As there are no statistical analyses that accompany these data, the confidence limits are an unknown factor.

Investigating a 32 km sector of a Japanese river, Okane (1978) noted that the number of watermold spores per sample increased during the late spring and in the autumn, but declined throughout the summer and winter months. On this basis, he classified *Achlya flagellata*, *Saprolegnia diclina*, and *S. ferax* as spring and autumn forms, and *A. megasperma*, *A. apiculata*, *Aphanomyces stellatus*, and *Pythiopsis cymosa* as winter species. Okane's observation on the occurrence of *S. ferax* is diametrically opposed to Stpiczyńska's (1962) claim for the seasonal occurrence of this species in Poland (see Table 17).

Not all field studies of the Saprolegniaceae in particular localities have yielded data supportive of alleged seasonal periodicity, Logvinenko and Meshcheryakova (1971), working in the Kharkov region of the Ukraine (50°N latitude), could not make out any definitive seasonal fluctuations among 53 species collected over a five-year period. Similarly, the records from the 1970(a) account of ecological research by Ristanović do not suggest that there was a pattern of seasonal occurrence among the Saprolegniaceae she collected. Only if one is content to use narrow temperature ranges can a case be made for seasonal occurrence of the watermolds collected by Staniak (1971) in four sites (stream, peat bog, and ponds with and without stocked fish) in Poland. An overall view of her data permits the conclusion that the species did not occur in relation to any water temperature changes accompanying annual seasons. Staniak's findings contrast sharply with those reported (also from studies in Poland) by Zabrowska (Fig. 9) and Stpiczyńska (Fig. 10). Talukdar and Baruah (1952) perceived no correlation between the appearance of watermolds in culture from samples of Indian river and the month those samples had been collected. Seasonal fluctuations in abundance may seem to exist for the most common species in a given site, as Dick (1962) has shown for *Aplanopsis terrestris*. Those watermolds recovered only occasionally in a given site often appear to be sporadically distributed as to season, and thus no periodicity can be detected for them.

Two publications on watermold ecology illustrate one of the troublesome complexities attending analyses of populations for possible seasonal occurrence. Forbes (1935b) observed that *Saprolegnia ferax* declined in frequency in samples taken during the winter, December through February, while at the same time in the same locality the number of isolations of *S. monoica*[†] were at their peak. Subsequently, the high and low frequencies were reversed for the two species. Within the context of Seymour's (1970) taxonomic view of *S. ferax* and *S. monoica*[†], the data accumulated by Forbes show clearly

that she was finding only one species, but one having forms with few antheridial branches (*S. ferax*) at certain seasons, and those with abundant antheridial hyphae (*S. monoica*) at others. Hunter's (1975) later observations corroborate those of Forbes; the *S. ferax* form of the "*ferax/monoica* aggregate" (Dick, 1969b) predominated in the summer, while the *S. monoica*[†] form was most frequent in colder winter waters.

Some investigators have reported data on seasonal periodicity of Saprolegniaceae only in terms of the frequency of occurrence of genera. Such information is patently too general to support meaningful analyses or comparisons, but the various accounts nevertheless warrant mention.

Thakur Ji and Dayal (1966) determined generic frequencies (over a ten month period) based upon numbers of propagules L⁻¹ of water sample. Specimens of *Achlya* were abundant in the summer and winter/spring samplings, and were common also in the autumn. Members of *Saprolegnia*, however, were isolated frequently from collections in the autumn and early winter months, but not in samples taken in July and August. With one exception, representatives of *Achlya* were always more frequently isolated than were those of *Saprolegnia*. This of course to some extent contradicts Höhnk's (1935a) theory of sporulation pattern as a corollary to an aquatic versus a terrestrial habitat (see Fig. 5, Chapter 4). Cultures of *Aphanomyces* were obtained by Thakur Ji and Dayal more frequently in winter samples than in those collected in other seasons.

Using a quantitative estimate of propagule numbers, Willoughby (1962) scored the weekly occurrence of generic representatives from samples at a lake margin. Counts of specimens of *Saprolegnia* were low in the period from December to March, and again in August and September, but were high in late summer and autumn (September-October). The maximum frequency of *Achlyas* was obtained from samples collected in October-January, but members of *Dictyuchus* were uniformly low throughout the year (Willoughby, 1962). The largest numbers of spores of *Leptolegnia* species appeared in the October, March, and July samples from the English lake, but it must also be recognized that individuals of this genus were generally very few in comparison to those of *Achlya* and *Saprolegnia*. Counts made by Clausz (1974) of the numbers of propagules in a North Carolina impoundment pointed to an abundance of representatives of *Leptolegnia* in samples taken in all but the warmer months.

As the foregoing account makes clear, most studies on the seasonal occurrence of the water molds simply show that there is or is not a coincidental relationship between presence of a fungus in a site and season or month, with scant heed paid to accompanying environmental factors. An exception appears in the report by Al-Saadi and his associates (1979). They traced annual fluctuations in the frequency of water molds and phytoplankton recovered from an Iraqi river. During the period when the phytoplankters were at their maximum the frequency of saprolegniaceous fungi was correspondingly lowest. Conversely, when the populations of the phytoplankters were demonstrably low, the water molds were at their peak abundance. Al-Saaid and his colleagues concluded that the water molds were dependent on dead (moribund?) phytoplankters as a nutrient source and that this accounted for the increase of fungi

following the decline of the planktonic species. The seasonal fluctuation of saprolegniaceous fungi in the river was alleged to be independent of pH, salinity, and dissolved oxygen. Whether an inverse correlation exists between saprolegnians and phytoplankton populations in other aquatic systems remains to be determined.

SEASONAL CLASSIFICATION

It will not seem unusual that saprolegniaceous species have been classified with reference to their periodicity or season of occurrence (for example, Érgashev and Kirgizbaeva, 1978; Domashova, 1974b; Kirgizbaeva *et al.*, 1975; Hunter, 1975; Maestres, 1977). Of course, any such scheme predicts for these fungi a fair degree of seasonal constancy which in fact they may not have.

Four of the published groupings of species according to season or prevailing condition are shown in Table 18. It is difficult to draw meaningful conclusions from data which, overall, show such diversity. There are to be sure some similarities evident in the seasonal species listings prepared by R. E. Roberts (1963) and Hunter (1975); both investigated sites in England. Data from the study of Maestres (1977) stand out only because species of *Achlya* appear to be rare in the Newfoundland river she sampled. Of particular interest in Alabi's listing (Table 18) is the absence of species of *Saprolegnia* in the habitats he sampled. This accords well with the findings of most other investigators (Rossey-Valderama, 1955, 1956; Scott, 1960a; Dogma, 1966) that species of this genus are rare in soils of tropical countries, save at high elevations. Although Alabi (1971b) recovered species of *Brevilegnia* rather frequently in his isolations, it should not be concluded that members of this genus are only tropical or subtropical in their distribution. They are relatively common in Iceland (T. W. Johnson, 1974a; T. W. Johnson *et al.*, 1973), for instance, a country oceanic but hardly tropical in its climate.

The study by Manoharachary (1979a) related occurrence of Saprolegniaceae in water to three seasons, winter, summer, and monsoon (wet). Like Alabi (1971b; *see* Table 18) Manoharachary found certain species to be "all season" ones (for example, *Achlya debaryana*), and some to be characteristic of the winter season (*A. orion*). The value of Manoharachary's investigation, however, lies in the fact that he measured particular physico-chemical factors (other than temperature) of the environment. *Achlya recurva*, a so-called "monsoon species" in terms of the season of its greatest abundance, was distributed primarily in relation to a high ammonia level in the water, a characteristic accompanying the rainy period. Seasonal occurrence of water molds, then, is not necessarily temperature-dependent.

The seasonal classification of Saprolegniaceae proposed by Khulbe and Bhargava (1977); (*see* Chapter 3) is of particular interest because it was based on a comparison of water molds from lakes in two climates, temperate and subtropical. They recognized four categories of species. The maximum yields of Saprolegniaceae from the two temperate lakes sampled appeared in the summer and autumn, while peak yields were realized in the spring and autumn in the three subtropical habitats they were just as common in the spring (March-April). Whereas Alabi (1971b) collected *Aphanomyces*

laevis, *Brevilegnia linearis*, and *Thraustotheca clavata* most frequently in the tropical dry season when water temperatures were high, Khulbe and Bhargava (1977) found these same species (in the Indian lakes) to be characteristic of constant, low temperature, and high temperature categories, respectively. The temperature ranges on which these later authors based the four categories overlap substantially, and for this reason their conclusions are open to question.

PERIODICITY IN SOIL AND SEDIMENTS

The majority of work on seasonal periodicity in the occurrence of the Saprolegniaceae has been centered around habitats with sampling being largely of water rather than soil. Very few published accounts suggest that water molds in soils and sediments may also show some degree of periodicity, but some investigations (Manoharachary, 1979b) on seasonality of water molds in pond sediments, yield data much too scanty to provide any convincing evidence.

Data from an investigation based upon periodic samplings in soils of southeast England, led Dick and Newby (1961) to conclude that seasonal fluctuation was evident for some species. *Achlya apiculata*, *A. spinosa*, *A. radiosa*, and *A. racemosa* were abundant in winter samples, but very infrequent in those soil samples taken in July and August. *Pythiopsis cymosa* was recovered most frequently in the spring, but was extremely uncommon in samples collected in the summer. This is certainly not in accord with what we find (unpublished records) in tropical Brazilian soils, for instance, from which representatives of the genus, including *P. cymosa*, are regularly and frequently recovered. In Iceland, at any season of the year, specimens of *Pythiopsis cymosa* have appeared only in samples of water or sediments in fish-rearing ponds, or on diseased fingerlings (Howard *et al.*, 1970). Although some mycologists have hinted at seasonal distribution as an expression of availability of nutrition (Park, 1972b; Dick, 1970), the possibility that this factor is a major one in determining the occurrence of water molds has not been explored adequately.

Suzuki (1961b) isolated several species of water molds from sediments of a Japanese lake over a period of about one year. *Achlya flagellata*[†], *A. racemosa*, and *Saprolegnia* sp., among others, were said to reflect a general trend in seasonal periodicity, namely, a high frequency of occurrence in the winter, and a correspondingly very low frequency in the summer. Although Ristanović (1970a) found that there were different periods of the year when certain species could be collected from sediments of the Yugoslavian river Stavna and its tributaries, no pattern of seasonal periodicity emerged from her data.

Using a quadrat method for sampling soil sites Prabhuji (1979) isolated water molds on a monthly basis and related recovery to temperature, pH, organic content, and moisture level. As others had reported (Table 18), he found particular species were predominant in samples taken at specified seasons, and was able to arrange those fungi into categories according to soil temperature. Low (19-24 °C) temperature species were *Achlya proliferoides*, *Pythiopsis humphreyana*, and *Leptolegnia*

sp., among others, while *A. orion* and *A. diffusa*, for example were moderate-temperature (25-30 °C) ones. He found no species characteristic of the season of high soil temperature (31-35 °C), and only two taxa of *Aphanomyces* could be classified as constant species, that is, ones occurring throughout the temperature range encountered during all seasons (19-35 °C). There were simply fewer recoveries of watermolds, Prabhuji noted, when soil temperatures were in the range of 32-35 °C.

OOSPORE TYPE AND PERIODICITY

It was A. W. Ziegler (1958b) who first suggested that a seasonal periodicity of Saprolegniaceae could be recognized if the oospore structure of species was taken into account. Subsequently, G. C. Hughes (1959, 1962) explored this concept in depth. He analyzed the existing literature and called attention to the fact that prior investigators -- beginning with Coker (1923) -- had actually encountered but not recognized this pattern. Some reservations have been expressed by Dick (1976) about the applicability to the concept of seasonal occurrence of the data from the studies by G. C. Hughes (1962), G. C. Srivastava (1967b), Milanez (1966), and Alabi (1971b), among others. Moreover, seasonal periodicity as expressed by occurrence of species of particular oospore types is evidently not of universal occurrence (Dayal and Tandon, 1962; Logvinenko and Meshcheryakova, 1971). It appears also that the geographical location of the sites sampled for watermolds influences significantly their ostensible seasonal periodicity. Maestres and Nolan (1978), for example, found species with centric and subcentric oospores to peak in frequency in the summer. Previously it had been supposed that such watermolds predominated in winter months, as G. C. Hughes (1962) had discovered. This apparent disparity is not particularly striking when it is recognized that Maestres and Nolan collected in Newfoundland (cool summers) and G. C. Hughes investigated watermolds in southern Georgia (hot summers). Nevertheless, there are a sufficient number of published reports available to save the observed phenomenon from outright denial -- whatever its cause.

Table 19 illustrates some of the collection data from which G. C. Hughes (1962) derived the conclusion that species with eccentric oospores do not exhibit a seasonal periodicity, while those with centric or subcentric ones clearly do (Fig. 6).

There is an impressive list of accounts (only some have an entirely acceptable data base) that ostensibly confirm this phenomenon, notably those of Apinis (1929a, b), Coker (1923), A. Lund (1934), Forbes (1935a, b), Beverwijk (1948), Dayal and Thakur Ji (1966), Dick and Newby (1961), Dudka (1965, 1966), Fox and Wolf (1977a) Klich (1980), Milanez (1966), Mushin (1977), Prabhuji (1979), Ristanović (1973), Sorenson (1962), TeStrake (1958), Toma (1969, 1971), and Zabrowska (1965). Supportive data compiled in some of these accounts are shown graphically in Figures 7-10.

Two reports of seasonal periodicity as reflected in species, oospore type are singled out because they deal in part with tropical and semitropical regions. In southern Nigeria, Alabi (1971a, b) found that watermold periodicity was related to moisture rather than temperature (Fig. 11): species with centric or subcentric eggs were

isolated only from samples collected during the rainy season (April to September). Water from temperate Indian lakes, Khulbe and Bhargava (1977) noted, yielded about 10% more species with centric oospores than those with eccentric ones. Data from samples of subtropical lakes, on the other hand, showed no substantial differences in the proportions of species with one or the other egg types.

It is by no means to be expected that species of Saprolegniaceae universally exhibit a relationship between oospore type and month or season of occurrence. In some geographical localities, at least, it appears that species with certain egg types are virtually absent. The list of water molds collected by Scott (1960a) in Haiti is a case in point: only forms with eccentric oospores were found there. Isolations made by Rossy-Valderama (1956) from soil samples of the El Yunque region of Puerto Rico yielded only one species with subcentric eggs, and none of the taxa with centric ones was recovered. Much farther north, in samples from a Newfoundland river, Maestres (1977) did not collect any members of *Achlya* with eccentric oospores during a year-long study. No patterns of periodicity in association with species of particular egg types have been observed in soils and waters of Iceland (Howard *et al.*, 1970; unpublished observations) where cool to cold temperatures prevail annually.

If it is accepted that there is a seasonal periodicity (perhaps, but not necessarily, reflected in the type of oospores of the species collected) in the occurrence of water molds, where are these fungi in those seasons when they do not appear in collections from the precise localities where they have been recovered at other seasons? No one has proposed an answer to this question, but perhaps Johannes (1957) and G. C. Hughes (1962) have formulated a partial response. Johannes demonstrated that sexual and asexual reproduction by water molds in an aquatic habitat fluctuated seasonally in response to temperature and oxygen levels. Oogonium production by representatives of the family which he trapped on submerged bait took place *in situ* in the coldest and most oxygen-rich zones in the lake he studied. Ismail *et al.* (1979) and Rattan and his associates (1979) reported that *Saprolegnia* species and members of *Dictyuchus* displayed sex cells when isolated from water at low temperatures, but in water at high temperatures members of these genera were predominantly asexual. Precisely how these differences were detected is not clear, yet they certainly seem to confirm Johannes' observations based on *in situ* baiting.

The experimental gross culture manipulations devised by G. C. Hughes (1962) appear to be an appropriate approach to the foregoing question. He collected samples of water and soil having an ambient field temperature of 9-15 °C. The samples were incubated at 15 °C until they had stabilized at that temperature, and then were subdivided. Half of each sample was held at 30 °C for 36 hours, the remaining portion being reincubated for the same length of time at 15 °C. All the samples were then baited and kept at 23-25 °C until water molds appeared. About half of the species recovered from gross cultures exposed only to 15 °C before baiting were ones with centric oospores, and about half were individuals with eccentric oospores. Only eccentric-egged species were collected from the half-samples exposed to 30 °C. Soils that had been kept at 30 °C prior to baiting were incubated at 15 °C for 36 hours and

then rebaited. Subsequently, some species with centric oospores appeared in those samples -- preincubated at 30 °C -- where none had previously been recovered. One may only speculate as to a reason for this yield response to incubation temperature, but it seems evident that -- for whatever reason -- species with different types of oospores are discernibly heterogeneous in germinability at particular temperatures. Perhaps the oospore types also have different thresholds of germination in response to the moisture level of soil. If so, the explanation for periodicity (as it seems to be correlated with oospore type) during dry versus wet seasons might be brought out by experimental work on soil moisture effects. The seasonal fluctuation detected in aquatic habitats, however, cannot be attributed to the influence of moisture, and an explanation must be sought elsewhere.

The experimental work, referred to in the foregoing paragraph did not provide the bulk of information that permitted Hughes to arrive at his theory of seasonal periodicity. The data supporting this concept came from an analysis of collections of two series of samples (500 total) taken at two different periods of the year, winter and summer. The 250 samples collected during winter were never allowed to incubate at a temperature above 22-23 °C during any stage of handling, and the summer samples were not allowed at any time to become cooler than this narrow temperature range. Thus, the "baiting" temperature in the main portion of Hughes' study was 22-23 °C. The temperature of the winter samples (at the time of collection) ranged from 7-22 °C; those of the summer samples were between 17 and 37 °C (224 of the 500 samples were at a temperature above 20 °C at the time of collection).

The only study specifically designed to repeat G. C. Hughes' (1962) experimental work was that of Dey (1969). He treated soil samples in precisely the same manner that Hughes had done, but sampled quite different sites. Dey collected repeatedly only in three localities, selected as to soil type and vegetational cover. Irrespective of incubation temperature (15 to 30 °C), water molds with eccentric oospores appeared in samples taken throughout the entire collecting period (approximately one year). Dey concluded that temperature did not influence periodicity because in laboratory culture at least, where incubation of samples was manipulated as Hughes had done, there were no detectable patterns evident among species producing centric or subcentric eggs. On the other hand, the field data (Dey, 1969) demonstrated that water molds with centric or subcentric oospores clearly predominated in the spring whereas those having eccentric oospores occurred regularly in samples taken at all three sites in the autumn and winter months. Thus, Dey failed to find a seasonal periodicity under laboratory conditions, but in the field such patterns obviously existed. As Hughes had sampled ten sites (with essentially no repetition) for his experimental work involving the manipulation of incubation temperature, and Dey explored only three areas, it is possible that this difference in the nature of sampling skewed the observed results. Perhaps by repeatedly sampling the same sites Dey was recovering species that were in aggregate patterns of distribution just as Dick (1962) had discovered in his earlier investigation.

AN ANALYSIS

While it must be admitted that ecological studies on the Saprolegniaceae (Chapters 3-5) are not barren of information, great gaps exist not only in the existing data but also in the explanation of occurrence, distribution, abundance, and frequency of these fungi. In spite of all that has been written about seasonal periodicity, for example, we find the subject deficient in convincing evidence. Dick (1976) has commented on the status of knowledge of the ecology of water molds, and we shall not presume to question or enlarge upon his conclusions. Two points, however, need emphasis.

First is the matter of sampling methodology. Very prominent differences exist in the data reported in studies on abundance and frequency of water molds in natural habitats, and an analysis of the accounts leaves no doubt that the discrepancies are attributable to a variety of factors: the number of samples on which observations are based, conditions extant at the sampling time, temperatures of culture incubation, and even different interpretations of ecological terms, to name a few. Accordingly, it is impossible to draw meaningful comparisons among the results of such research, yet without such comparisons explanations for particular responses to environmental conditions and community composition surely cannot emerge. If it appears that the record of achievement in the ecological research on the Saprolegniaceae is one of bits and pieces, this is precisely because uniformity in approach has not been attained, or proper experimental design, supported by statistical analyses to corroborate the validity of results, has not been achieved. A task of first priority, then, is to devise methodology and intelligent use of statistical principles that, when broadly adopted, will bring a degree of consistency to the manner in which data are gathered. Some methodological standardization could help to provide a base for comparative analyses, and conclusions drawn from results would then reflect primarily differences in interpretation, not technology. Sound knowledge of the ecology of the Saprolegniaceae is elusive because both the technology used to gather data and the subsequent interpretation of them are vexatiously inconsistent.

A second point requiring attention is that of the ecological activity of water molds, a matter which we have all but avoided in these chapters. There are incidental -- and not so incidental (Dick, 1976) -- references in the literature (Newton, 1971) which suggest that these fungi are at times active members of communities and at others passive components. Chiefly, we do not dwell on these published accounts that deal with activity simply because there is so much divergence in the use to which the term "activity" has been put. It is employed with various connotations: recitals of likely metabolic and regulatory roles for these fungi in the natural community on the one hand, to, on the other, whether or not they grow vegetatively there or only pass the time until conditions for reproduction permit them to move on to more appropriate environs. Simply knowing the diversity of saprolegnians existing at a given time in a given habitat is in no way predictive of their physiological activities there, yet this is the meaning of activity conveyed in some accounts. Presumably the water molds function

in nature as do other fungi in theirs -- the exploitation and thereby the cycling of deposited organic matter. The task holding second priority, then, must be that of defining clearly the parameters of "activity" as they are applied to saprolegiaceous fungi, and diligently devising means to measure and evaluate them in habitats where they occur.