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The abundance of algal species and their parasites was monitored weekly for two years in a sewage lagoon at the Corvallis Airport, Oregon. During the cooler months, Euglena species were dominant followed by a Chlamydomonas assemblage in the spring and a predominantly Scenedesmus assemblage in the summer and fall. Parasites infected 14 of the 35 most abundant species of algae. An unidentified chytrid parasitized Scenedesmus obliquus, and a Rhizophydium sp. infected Chlamydomonas species. The most common parasite, Aphelidium chlorococcarum Fott, infected 11 species, particularly species of Scenedesmus. Aphelidium chlorococcarum was isolated in culture for morphological

and ultrastructural study. Reclassification of Aphelidium as an Olpidiaceous chytrid was recommended.

Only very severe infections had a significant impact on host populations and these were rare. Aphelidium chlorococcarum infected less than 10% of the host populations most of the year. The most severe infection observed (74%) was followed by a sharp decrease in the population of S. armatus for a month. Other declines after severe parasitism were small and lasted approximately one week.

Certain climatological, chemical, and biological factors were related to the occurrence of severe infections. Of these, a dense host population favored severe parasitism the most. Increased precipitation was also associated with severe infections in the fall.

Responses of Algal Populations to Parasitism by *Aphelidium chlorococcarum* and Chytrids in an Oregon Sewage Lagoon

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INTRODUCTION

As the world population increases, so does the need for the more efficient use of diminishing resources. Current wastewater treatment methods are expensive and waste valuable nutrients which could be recovered by harvesting algae grown in the sewage. Algae are a concentrated source of high quality protein that can produce greater yields per acre than any other agricultural crop (Venkataraman, 1969). Culturing algae in wastewater is appealing since it is inexpensive and it simultaneously addresses the issues of waste disposal, nutrient recovery, water purification and new sources of protein.

Research on the culture of algae in wastewater began in the 1950's (Oswald et al., 1953). Since then, demonstration ponds have been built in the USA, Israel, India, Australia, the USSR, Singapore and the Philippines. A lack of economical harvesting methods and inadequate knowledge of the dynamics of predation and parasitism of algal populations have prevented the general implementation of this system (Yang et al., 1980; Shelef & Soeder, 1980).

Parasitism by fungi, bacteria and viruses is known to be one factor which influences the abundance of algal species in natural aquatic habitats (Canter and Lund, 1969; Lund, 1957). In mass cultures of algae, parasitic fungi sporadically reach epidemic proportions and sometimes destroy the culture (Soeder and Maiweg, 1969; Fott, 1967). Little is known of the factors that trigger epidemics. Researchers have typically approached this question by attempting to correlate changes in environmental parameters with the occurrence of epidemics in natural habitats (Canter and Lund, 1969; Masters, 1976). Now that some of the parasites have been successfully cultured, a few authors have begun laboratory experiments to study the factors favoring parasitism (Barr and Hickman, 1967; Abeliovich and Dikbuck, 1977; Canter and Jaworski, 1981).

This study is the first to examine the fluctuations of algae and their parasites, primarily Aphelidium chlorococcarum, in a domestic sewage lagoon. The importance of parasitism for regulation of the fluctuations of algae was assessed by relating changes in the abundance of host species to the occurrence of severe infections. The results were similar to those of studies of chytrids infecting diatoms in lakes. Parasitism was much less important than climatic factors for the regulation of the periodicity of host species.

Of the factors investigated that might favor epidemics, host density was of overriding importance. Increased precipitation also seemed related to epidemics in October and November.

The most abundant parasite in the lagoon, Apheli-dium chlorococcarum was successfully cultured on algal hosts in the laboratory. Culture facilitated study of the life history and observation of ultrastructural details of the parasite. Reclassification of Apheli-dium, which has been considered a protozoan, to the Olpidiaceous chytrids was recommended.

The Corvallis airport sewage oxidation pond was selected for study partly because of its proximity to the researcher. Furthermore, the pond treats only domestic sewage from lavatories at the airport, rather than industrial sewage which may have toxic components that would make it unsatisfactory for the culture of algae. This lagoon was ideal for studying the para-sites of algae that occur naturally in a low technology system where algae might one day be cultured for har-vest. Parasites that infest commercially valuable species of algae in the natural biota are likely to reduce productivity in large scale cultures of these algae. Control of these parasites will be facilitated by understanding their dynamics in natural systems.

LITERATURE REVIEW

The impact of parasites on algal populations in aquatic ecosystems is not easily assessed. In order to estimate the relative influence of parasitism on algal succession, one must know something of the other factors that regulate succession. Factors that may be involved have been listed by Keating (1976) and others. These include physical and chemical factors such as light, temperature, rainfall, nutrients, oxygen and CO_2 concentrations; and biological factors such as grazing, parasitism, competition, allelopathic inhibition and metabolic effects. Yet, despite years of study, phytoplankton succession is still poorly understood.

> Limnologists have addressed themselves for more than fifty years to the distribution of phytoplankton and their biomass in relation to environmental factors in lakes of different trophy. Although this activity has resulted in an enormous and still rapidly growing literature, progress in understanding and prediction has been very slow. ...Few predictions can be made about the composition and pattern of succession of the species or groups making up this biomass.
>
> (Kalff and Knoechel, 1978, p. 475)

Kalff and Knoechel believe that the slow progress is in part due to the many possible factors and partly to inadequate methods for their evaluation. Algal succession is likely a response to the interactions of many of the above parameters as well as other factors. One commonly cited model for the classic spring and fall

phytoplankton growth cycle is that the factors of overriding importance are light, temperature and nutrients (Reynolds, 1973). Growth occurs when these are favorable. Declines occur in summer because of nutrient depletion and in winter due to unfavorable light and temperature conditions. This remains a widely held view although numerous other factors have been shown to influence algal succession in some circumstances. For example, field studies of fungi parasitic on algae have demonstrated that parasitism can reduce host populations appreciably (Canter and Lund, 1969).

Parasites of Freshwater Algae

Viruses, bacteria and fungi are known to parasitize freshwater algae. Most of the literature on this subject consists of taxonomic descriptions of Chytridiomycete fungi. Viral and bacterial parasites of algae have been discovered only recently and less is known of these groups than of fungal parasites. The following sections will review the literature on each of these groups of parasites, especially relative to their influence on host populations and their distribution in nature. In a later section, evidence from laboratory experiments on environmental factors that may favor fungal epidemics will be summarized.

Viruses

A few viruses of eukaryotic algae have been reported (Gibbs et al., 1975; Hoffman and Stanker, 1976). For example, a phage-like virus infected the zoospores of *Chlorococcum minutum* (Gromov and Mamkaeva, 1979, 1981). Not much is known of these organisms. For the most part, viruses have been found on filamentous Cyanophyceae. Other than a report of a virus on *Anabaena variabilis*, (Mamkaeva et al., 1980), only the LPP viruses are known.

LPP cyanophages (termed LPP from the host generic names) are the most researched of the viruses that infect phytoplankton. Safferman and Morris (1963, 1964, 1967) first isolated viruses that infected *Lyngbya*, *Phormidium* and *Plectonema* -- all filamentous Cyanophyceae which were later classified as *Schizothrix calcicola* by Drouet (1963). Subsequent surveys revealed the broad geographic distribution of LPP viruses: in 11 of 12 Indiana sewage stabilization ponds, rice fields and a sewage pond in India (Singh, 1973). Daft et al. (1970) also found an LPP virus which was widely distributed in Scotland. Shane, et al. (1972) noted that all of the early isolations were from eutrophic water. Investigation of the distribution of these viruses by Shane (1971) showed they were

found in rivers, ponds and lakes, but not in the headwaters of streams. Samples collected from the upper Christina River in Pennsylvania lacked LPP viruses. Their numbers increased downstream as turbidity, hardness, iron, coliforms and biological oxygen demand (BOD) increased (Shane et al., 1972).

The relationship between LPP cyanophages and their hosts has been studied in continuous culture. Cannon et al. (1976) found that inoculation of a sensitive host strain with LPP virus in continuous culture resulted in a simultaneous decline in host cells and increase in viral titer. The viral numbers then declined to a stable minimum as the host returned to a stable maximum. In one case, three oscillations were reported before the system stabilized. Cannon's explanation of the damped oscillation was that resistant host cells were selected as a result of the death of the sensitive hosts. Maintenance of low but constant levels of virus in the chemostat implied the continued "evolution" of sensitive host cells. He suggested multiple oscillations could result from rapid viral and/or host mutations that altered susceptibility of the host or virulence of the virus. As expected, the addition of virus to a resistant host strain had no effect on the host numbers, which remained stable, and

the viral numbers decreased rapidly as they were washed out of the system.

In another study of LPP phages, Lindmark (1979) investigated several factors affecting the severity of infection: pH, age of host culture, host density and the presence of other algal species in static culture. The host cells were more resistant to viral infection at pH values above 11 which occurred in dense host cultures. The addition of other algae, Scenedesmus or Anabaena, to the cultures had no effect on the viral replication rate. The most noticeable effect was that the host culture in the log phase of growth supported the fastest initial replication rate. But, after 10 days, the number of plaques was the same in cultures of all ages.

Bacteria

Bacterial pathogens of a variety of Cyanophyta have been reported from fresh water in Israel, the USA, Sweden, the USSR, and the United Kingdom. These include Myxobacteria (Daft and Stewart, 1971; Daft et al., 1975; Shilo, 1966, 1970; Stewart and Brown, 1971), Flexibacteria (Gromov, et al., 1972), a Bacillus (Reim et al., 1974), Cytophaga (Stewart and Brown, 1969), and Cellvibrio (Granhall and Berg, 1972). Also Bdellovibrio bacteriovorus was found lysing Phormidium luridum

and Synechoccus sp. (Burnham, et al., 1976, 1977). Only one green alga, Chlorella vulgaris, has been found to be parasitized by a bacterium, Bdellovibrio chlorellavorus (Gromov, 1972a; Mamkaeva and Rybal'chenko, 1979). Gromov (1980) proposed this organism be renamed Vampirovibrio chlorellavorus.

Most of the research on bacterial pathogens has focused on taxonomic characterization. Daft et al., (1975) studied the distribution of these pathogens, their importance in the regulation of algal blooms, and their host specificity. They were widespread in lochs, reservoirs, a sewage plant and alkaline soil where the hosts were abundant. There was no evidence that these bacteria play an important role in the lysis of blue-green blooms. Their host range is less specific than that of viruses. Some can be grown on organic substrates in the absence of the hosts. Environmental factors that Daft et al. (1975) found were favorable to lysis included high dissolved oxygen concentrations, a pH of 7-9, elevated temperatures (up to 30^{o}C), high organic content of the water, and abundant host cells.

Aphelidium

Because the taxonomic position of this genus that was so abundant in the sewage lagoon is uncertain, the

literature on this genus will be considered separately from that of the fungi. See the description of Aphelidium for a discussion of the taxonomic status of this organism.

The distribution of Aphelidium in nature has not been studied extensively. Zopf (1885), Scherffel (1925), Fott (1954, 1957) and Gromov (1972b) found Aphelidium parasitizing various algae in European ponds and lakes as well as a ditch and a river in Russia. Canter and Jaworski (1978) observed Aphelidium in Lake Windermere, England. Schnepf et al. (1971) and Gromov and Mamkaeva (1970) found A. chlorococcarum in mass algal cultures on Scenedesmus armatus and Kirchneriella obesa respectively. These authors did not elaborate on the impact of Aphelidium on the cultures. Fott (1957) observed Aphelidium commonly in Czechoslovakia and thought it was probably cosmopolitan.

The few Aphelidium strains studied appear to be relatively host specific. Most are virulent on only certain strains within a few genera. Fott (1957) found that only 4 of the 8 species of Scenedesmus and Chodatella and none of the 9 other Chlorococcalean genera observed were infected by A. chlorococcarum in a lake in Germany. In a mass algal culture containing a mixture of Scenedesmus armatus and S. acutus var. alternans, Aphelidium chlorococcarum only parasitized

the former species (Schnepf et al., 1971). Gromov (1972b) and Gromov and Mamkaeva (1970) did the most comprehensive host range studies to date on two Apheli-dium species. A. chlorococcarum f. majus infected only 4 strains of Ankistrodesmus and 2 strains of Kirch-neriella out of 30 genera represented by 248 strains of algae tested. A. tribonemae parasitized only the yellow-green algae: Tribonema spp., T. gayanum, Chloridella neglecta, and two strains of Botridiopsis intercedens.

Fungi

Fungi parasitize many of the fresh water algae including diatoms, desmids, dinoflagellates, green algae, cryptomonads, and blue-greens (Sparrow, 1960; Karling, 1977). Most of these parasites belong to the Chytridiales (chytrids). A few are in other groups such as the Lagenidiales and Blastocladiales. Chytrids have been found parasitizing algae in as diverse habi-tats as barn siding and snow. They probably occur wherever the hosts are found (Masters, 1976).

Impact of Chytrids on Algae

Impact in natural aquatic systems

Canter and Lund (1948, 1951, 1953, 1969) were the first to critically investigate the fluctuations in numbers of algal hosts relative to their fungal parasites. Their data spanned twenty years, providing the most comprehensive basis to date for the characterization of epidemics and the estimation of the importance of parasitism. They established that parasites are one important factor which determines the structure of a phytoplankton community. Lund has summed up the role of parasitic fungi.

> Over a large part of the year, but few of the host population are infected. Sometimes, however, the fungi multiply rapidly, faster than the algae so that the infection reaches epidemic proportions with a consequent decrease in the algal population.
>
> (Lund, 1957, p. 19)

Canter and Lund observed the following characteristics of epidemics. (1) They occur sporadically. One year they may be severe, the next year non-existent. (2) Epidemics seem to be favored by the presence of large numbers of host cells. (3) In a typical epidemic, such as Rhizophydium planktonicum parasitizing Asterionella formosa, the abundance of the parasite closely paralleled changes in the abundance of the

host. The maximum percentage of infection coincided approximately with the host maximum. (4) The duration of epidemics was typically a few weeks and (5) afterward, the host population often resumed rapid growth if other environmental conditions were favorable.

The impact of parasitism on the host species was secondary to the normal seasonal periodicity of the hosts. The main impact was a decrease in the abundance of the host species, but notably not the loss of the species from the plankton. Canter and Lund (1969) postulate that this is because of the improbability of parasite zoospores encountering all available host cells when the host becomes scarce. The survivors are then able to rapidly reestablish the host population.

An example of the impact of parasitism on host abundance was the infection of Asterionella formosa, a dominant in the Windermere Lake phytoplankton, by Rhizophydium planktonicum. In the absence of epidemics, Asterionella exhibited spring maxima of approximately 10,000 cells/ml. The effect of fungal epidemics was to delay the time of the algal maximum, and when other environmental factors were unfavorable to the host, the size of the maximum was decreased as well. In the years 1946-1951, when more than 30% of the host cells were infected, Asterionella numbers did not exceed 325 cells/ml (Canter and Lund, 1953).

Usually the hosts declined more rapidly the more severely they were parasitized, but this depended on the relative growth rates of the host and parasite. For example, Canter and Lund (1969) found Staurastrum cingulum cells were dividing rapidly so that even when 40% of the host cells were infected, their numbers did not decline. As soon as the cell division rate of the host fell, infection rose to 92% and the number of host cells declined rapidly.

Subsequent observations have confirmed those of Canter and Lund. Epidemics of chytrid parasites are sporadic; they occur mainly when the host is relatively abundant and growing rapidly. The host numbers are reduced by severe epidemics but may either resume prior levels or decline for reasons other than parasitism. Severe parasitism occurs relatively infrequently (Masters, 1976; Reynolds, 1973; Van Donk and Ringelberg, 1983). The main impact of parasitism on phytoplankton populations is on the relative abundance of individual species. The number of host cells is reduced and this favors the increase of other species (Reynolds, 1973; Van Donk and Ringelberg, 1983).

Recent field studies have addressed the issue of the relative influence of physical, chemical and biotic factors on phytoplankton succession. In a study of a

small eutrophic lake, Reynolds (1973) concluded that physical, rather than chemical or biotic factors exert the main control over diatom growth. However, diatom species dominance may be modified by attacks of fungal parasites. Youngman et al. (1976) found that limitation of available silica was more important than parasitism in the decline of Asterionella, while parasitism appeared to be the primary factor in the demise of Closterium. Van Donk and Ringelberg (1983) supported the view that succession of diatom species is influenced by interacting factors. In their study, the initial reduction of Asterionella by parasitism favored the increase of other diatom species which ordinarily could not compete successfully with Asterionella for phosphorus.

Impact in mass cultures

Whereas in natural systems the impact of parasitism usually is not devastating, the impact of parasitism on algal monocultures can be quite severe, and could certainly become of economic importance if algae were cultured on a large scale. In Czechoslovakia, Fott (1967) observed a substantial decrease in a mass culture of Scenedesmus quadricauda due to parasitism by a chytrid, Phlyctidium scenedesmi. Eventually the culture had to be terminated and disinfected. The

parasite recurred when the culture was started again in a few weeks, perhaps because resting spores survived the disinfection process. Several years later, Phlyctidium scenedesmi reappeared in the same culture unit on Scenedesmus obliquus (Lukavský, 1970). The culture was invaded rapidly and the parasite was also found on other algal contaminants in the culture: Chlorella sp. and S. quadricauda. Again the culture had to be stopped for disinfection.

Soeder and Maiweg (1969) observed parasitism of two Scenedesmus species in mass cultures. The predominant species, Scenedesmus acutus f. alternans, was infected by Phlyctidium scenedesmi var. acuti which caused a sharp decline in the host abundance. A minor contaminant, S. armatus, then became dominant but was not infected until five days after it reached a maximum density. This parasitized host was replaced by the original species which did not become infected again until the relative abundance of the original host reached 98%. Shortly after this, the culture was terminated and disinfected with a fungicide. The authors hypothesized that two host-specific varieties of the fungus were involved because the hosts were not infected simultaneously.

Abeliovich and Dikbuck (1977) studied parasitism in Israeli sewage oxidation ponds where they found about 1% of the Scenedesmus obliquus cultured in the sewage were usually infected by a Chytridium sp. The infection sometimes "burst out into epidemics, causing a massive die-off of the algae".

Environmental Factors That Favor Chytrid Epidemics

Although chronic low levels of parasitism by chytrids are common, these are interrupted by sporadic epidemics. The factors that precipitate epidemics are not known. Several authors have attempted unsuccessfully to correlate changes in environmental variables with the onset of epidemics in natural aquatic systems (Canter and Lund, 1948, 1951, 1953, 1969; Paterson, 1960; Masters, 1971a-e). Canter and Lund examined seasonal parameters including: light intensity, daylength, temperature, rainfall, and thermal stratification. They also investigated the chemical parameters silica, nitrate, phosphate, and dissolved oxygen concentration. In addition, biological factors studied were: competition with other phytoplankton, density of host population, and the vigor of the host population. The results were inconclusive and they suggested that other factors precipitated the epidemics. Seasonal factors were apparently not critical since epidemics

were observed throughout the year. Because epidemics occurred most frequently in the more eutrophic lakes, they hypothesized that chemical factors might be involved. An additional hypothesis was that the initial products of resting spore germination were more virulent than other zoospores of the parasites thus resulting in sporadic epidemics. This could explain the apparent absence of a correlation between environmental factors and epidemics.

Masters (1971 a-e) found no correlation between epidemic periods and pH, conductivity, alkalinity, hardness, or the size of the host population. She hypothesized that the relationship between environmental factors and epidemics might be obscured if environmental conditions during the initial period of zoospore encystment are more critical than those during the later phases of infection. Her evidence that temperature may influence the onset of epidemics will be discussed in the section on temperature which follows.

Paterson (1960) studied these same variables, as well as dissolved oxygen, in relation to parasitism by Rhizosiphon on Anabaena in Frains Lake, Michigan. However, no epidemics were observed; the highest percentage of infection was only 0.5% of the host cell population. So, although a decrease in dissolved

oxygen coincided with an increase in parasitism, the results were inconclusive.

Canter and Jaworski (1981) pointed out the need for experimental study of the factors that precipitate parasite epidemics. Few laboratory studies have been possible because many of the parasites have not been successfully cultured. The results of experimental research on the variables that may be important in the occurrence of epidemics are summarized below.

Light

Three separate laboratory studies have established that light is required for some stage of infection by several chytrids. Canter and Jaworski (1981) found that the zoospores of Rhizophydium planktonicum require light for zoospore encystment on Asterionella formosa in laboratory culture. Once encystment occurred, the development of infection could continue in the dark. Abeliovich and Dikbuck (1977) showed that parasitism of Scenedesmus obliquus by a Chytridium sp. requires light of wavelengths 620-680 nm, the major wavelengths needed for photosynthesis. Barr and Hickman (1967) investigated factors influencing parasitism of Rhizophydium sphaerocarpum on Spirogyra and found that low light (less than 40 foot-candles) inhibited infection. In this case, the zoospores encysted but did not germinate

on hosts in the dark. The highest infection rate was obtained when the host was in the dark for 48 hours prior to inoculation, followed by one week of light. Darkness after inoculation considerably reduced the percentage of infection. In contrast, when the chytrid was grown in pure culture, rather than on the host, its growth was inhibited by increased light. Barr and Hickman (1967) also varied daylength from 8 to 16 hours and found that photoperiod had no effect on infection.

Oxygen concentration

In field studies, Paterson (1960) found that the periods of infection by Rhizosiphon coincided with a decrease in oxygen content of the lake water from 100% to about 90% saturation. Canter and Lund (1948) noted that the concentration of oxygen in the English Lakes was near saturation most of the time, yet epidemics were sporadic. They found preliminary evidence that aeration of lake samples increased the number of zoospores and live sporangia as well as the percentage of Asterionella cells infected by Rhizophidium. In laboratory experiments, Abeliovich and Dikbuck (1977) found that either saturation or anaerobic conditions prevented the infection and lysis of Scenedesmus obliquus by a Chytridium sp. They also found that some parasitism occurred in the dark unless glucose was

supplied. The addition of 0.5% glucose inhibited parasitism in the dark. They postulated that glucose increased the respiration rate of Scenedesmus which reduced the oxygen concentration to below the level required for parasitism. They believed that oxygen concentration was the fundamental factor influencing infection rates and that the inhibiting effect of darkness was the result of reduction of oxygen concentration by the cessation of photosynthesis. They hypothesized that in sewage ponds, epidemics would occur when BOD was lower as this would prevent anaerobic conditions from occurring at night.

Temperature

Several authors have suggested that temperature is a factor in the occurrence of chytrid epidemics. In a non-quantitative, 10-year study of Lake Geneva, Pongratz (1966) suggested that epidemics were related to cold weather. Fott (1967) observed the most severe epidemic during a cold, rainy summer. Masters (1971d) found that a delay in the appearance of Chytridium deltanum in the phytoplankton occurred during a year when the water warmed more slowly than in other years. The percentage of infection by Phlyctidium was lower in the coldest of the three summers, although this was not

true of Chytridium species. In contrast, Paterson (1960) and Canter and Lund (1948) found that parasitic fungi were tolerant of a wide temperature range in the field and that increases in infection rates were unrelated to temperature. Canter and Lund observed epidemics both under ice and at 14°C and the fungus was present whenever appreciable numbers of host cells were observed. Soeder and Maiweg (1969) observed a severe epidemic just after the water temperature increased in an outdoor culture.

In addition to the above field observations, temperature has also been studied in several laboratory experiments. Barr and Hickman (1967) concluded that temperature was the most important factor associated with epidemics. The optimum temperature for growth of the fungus Rhizophidium sphaerocarpum on Spirogyra was higher than the optimum temperature for growth of the susceptible host strain. The resistant host strain grew well at the temperature optimal for the parasite. They concluded that any environmental conditions unfavorable to the host would favor parasitism.

Van Donk and Ringelberg (1983) studied the effect of temperature on the parasitism of Asterionella formosa by Zygorhizidium planktonicum. Laboratory experiments confirmed their field observations that temperatures below 4°C inhibited fungal activity, while the

host continued to grow at low temperatures. As temperature increased, the rate of infection increased and the number of host cells consequently decreased. In their field observations, the interaction of temperature, stage of development of the fungus, and host population density seemed to determine the severity of infection. A severe fungal epidemic on Asterionella formosa was observed just after ice on the lake melted in 1979, but not in 1978. Ice had covered the lake for a longer period in 1979, which seemed to allow the resting spores of the fungus time to mature, while ice only covered the lake for 2 weeks in 1978. The host grew and was uninfected for two weeks in 1978, possibly because the resting spores were not mature enough to germinate at the time the temperature increased.

In summary, field observations on the relationship of temperature changes and epidemics are contradictory. In the laboratory, temperatures near freezing seem to inhibit fungal activity, which increases as temperature rises. It seems likely that temperature interacts with other factors, such as the stage of maturation of resting spores, to determine the onset of epidemics.

Hydrogen Ion Concentration

Paterson (1960) found that Rhizosiphon parasitism

occurred in a lake when the pH was 8-9, but this pH value did not necessarily result in increased infection. Masters (1971d) also failed to show a relationship between pH and epidemic periods. Barr and Hickman (1967) studied the pH requirements of a host and parasite in separate cultures and found that Spirogyra was tolerant of a wider range of pH than its parasite, Rhizophydium sphaerocarpum. The effect of pH on the percentage of infection was not investigated.

Cations

Abeliovich and Dikbuck (1977) showed that under laboratory conditions, Mg^{++} and K^{+} at concentrations of $10^{-2}M$ or higher inhibited infection of S. obliquus by Chytridium sp. while Ca^{++} and Na^{+} had no effect at any of the concentrations tested. Infection was inhibited by a medium in which most of the Na^{+} was replaced by K^{+} and the Ca^{++} concentration was low, although the host cells grew well in this medium.

Nutrients

A few observations suggest that nutrients may be a significant factor in the occurrence of epidemics. Canter and Lund (1948) noted that of four lakes which varied in nutrient concentration, epidemics were more frequent in the more eutrophic lakes. However, epi-

demics occurred both when the concentrations of nitrate, silicate and phosphate were high and when they were low during thermal stratification. No information was available on other nutrients that may have favored fungal parasitism. Fott (1967) reported preliminary evidence that Phlyctidium did not reproduce in a medium containing only inorganic nitrogen as the nitrogen source. At the same time, the parasite grew rapidly in outdoor cultures where urea was the nitrogen source. In laboratory experiments, Barr and Hickman (1967) found that infection of Spirogyra by Rhizophydium increased in the more dilute concentrations of soil-water extract. None of these studies provided conclusive evidence that nutrient concentration was directly related to the occurrence of epidemics.

Host growth rate and density

Canter and Lund (1969) concluded from 20 years of observations that a large number of host cells was one of the factors most conducive to parasitism by chytrids. Severe parasitism occurred only when the desmid abundance exceeded one cell/ml or the abundance of Asterionella exceeded 10 cells/ml (Lund, 1957). This was corroborated by Masters (1971c) who found that epidemics of Staurastrum only recurred when the hosts

were relatively abundant. The converse is not true -- a large number of hosts does not always result in parasitism (Masters, 1971e). Soeder and Maiweg (1969) found a similar pattern for parasitism in mass cultures of algae. The hosts were free of parasites until the host population became dense. Lund (1957) postulated that below a certain host density, the host cells are too far apart for the fungal zoospores to encounter hosts frequently enough to result in epidemics.

The host growth rate may be as important as its density. Heavy parasitism is often observed on rapidly growing host populations. Masters (1971d) suggested that parasite growth may be dependent on chemostimulation by exudates from rapidly growing hosts. Late in an epidemic, she had observed encysted zoospores of Chytridium deltanum with long germ tubes not in contact with a host cell. Reynolds (1973) suggested that the percentage of hosts infected is larger if parasitism begins earlier in the host increase. In contrast, one laboratory investigation favored the hypothesis that rapidly growing hosts are more resistant to infection (Barr and Hickman, 1967). They inoculated cultures of Spirogyra varying in age from 2 to 14 weeks with Rhizophydium sphaerocarpum. The percentage of infected host cells increased progressively in the 4 to 12 week old cultures where the host growth rate was slower than in

the younger cultures. Interpretation of this experiment is complicated by the probability that the host density also varied in these cultures. Further experimental studies are needed to understand the importance of host density, age, or growth rate on the occurrence of epidemics.

Host-strain susceptibility

There are many reports of algal species that include strains both susceptible and resistant to a single parasite. Gromov and Mamkaeva (1969, 1970) and Gromov (1972b) have tested the host range of Aphelidium and Amoeboaphelidium in the laboratory and have found that commonly within individual host species, both susceptible and resistant strains occur. Others (Koob, 1966; Masters, 1971c) have made similar observations on natural populations of the host species Asterionella formosa and Staurastrum pinque respectively. Barr (1967) studied susceptible and resistant strains of Spirogyra in laboratory experiments. In some instances, strain susceptibility is associated with some morphological difference, such as frustule length in Asterionella (Koob, 1966). More often, however, the host strains are indistinguishable morphologically. Masters (1971c) pointed out that natural populations of algal

species may consist of a mixture of susceptible and resistant strains whose proportion might vary at different times. This could explain the apparent sporadic nature of fungal epidemics which would appear when the number of susceptible host cells was higher than that of resistant hosts. If a susceptible strain could not be distinguished morphologically from a resistant strain, it would be easy to conclude erroneously that favorable environmental conditions resulted in the sudden appearance of an epidemic when actually a change in the genetic constitution of the host population was the precipitating factor.

Summary

Viruses, bacteria, fungi and Aphelidium, an organism of uncertain taxonomic status, are known to parasitize fresh water algae. The prokaryotic blue-greens are mainly parasitized by viruses and bacteria, whereas eukaryotic algae are parasitized by a variety of fungi -- especially Chytridiomycetes -- and by Aphelidium. All of these parasites appear to be widely distributed in diverse habitats. There is preliminary evidence that parasites of algae are more common in eutrophic water.

The impact of parasitism on the abundance of host species has been assessed mainly for the Chytridio-

mycete fungi. In large-scale cultures of single species of algae, the impact of fungal parasites can be severe, causing massive destruction of the host population. In natural aquatic habitats, parasitism is one of many factors that are secondary in importance to physiochemical factors in the regulation of individual species abundance. Episodes of severe parasitism are infrequent and brief, typically less than a few weeks. The more severe the infection, the greater the decline in the host species abundance. If environmental conditions are favorable, the host species resumes growth after a severe infection.

The factors that favor episodes of severe parasitism are not known. In one study, infection by viruses was greatest when the host was in the log phase of growth (Lindmark, 1979). A study of bacterial lysis of blue-greens indicated that infection was favored by abundant host cells, high organic content of the water, high dissolved oxygen and elevated temperature (Daft et al., 1975). Factors that favor parasitism by chytrids have been investigated most extensively in field studies. Field studies have been inconclusive, although in some instances, very low temperatures in combination with the stage of development of the parasite may have been important. Dense host populations

favor parasitism more than any of the other factors investigated in the field.

The few laboratory studies to date suggest that several parameters may be important in the occurrence of chytrid epidemics. Among these factors are: a minimum light intensity for encystment and germination of the parasite, high dissolved oxygen concentrations, and requisite temperatures for both the host and parasite. There is no conclusive evidence regarding nutrient concentrations, but high levels of organic material may favor parasitism. Factors relating to the host seem to be of prime importance. There is some laboratory evidence that parasitism is favored by abundant susceptible host cells, host populations in the log phase of growth, and initiation of parasitism earlier in the host increase.

Research on Aphelidium species has focused on taxonomic characterization, ultrastructural studies, and some host range observations. The periodicity of Aphelidium in natural habitats or sewage ponds has never before been studied, nor have the factors that precipitate epidemics of Aphelidium.

DESCRIPTION OF THE SEWAGE LAGOON

The sewage oxidation lagoon is located on the property of the Corvallis airport 8 kilometers south of Corvallis, Oregon. The lagoon has diameter of 90 meters and a depth of approximately 1 meter and is divided into two ponds (Fig. 1). No records exist of the bottom of the lagoon having been dredged. A thick layer of sediment has accumulated that is easily re-suspended by wind action resulting in a marked increase in turbidity. The general appearance of the lagoon is that of a small pond with ducks and other birds nesting among the cattails along the banks. The odor of sewage is rarely detectable and then only near the influent station in Pond I. Pond II differs from Pond I in that it receives already partially oxidized sewage from Pond I and it is stocked with a large population of Gambusia sp. introduced to control mosquito larvae.

The lagoon has treated domestic waste from the airport for over 30 years. Domestic sewage from the airport lavatories is collected in two holding tanks with a retention time of less than 30 minutes. Then it is pumped into Pond I at station A (Fig. 1). The average rate of flow into the lagoon is 114 cubic meters/day in winter and less in the summer. After the initial aerobic oxidation by microorganisms in Pond I,

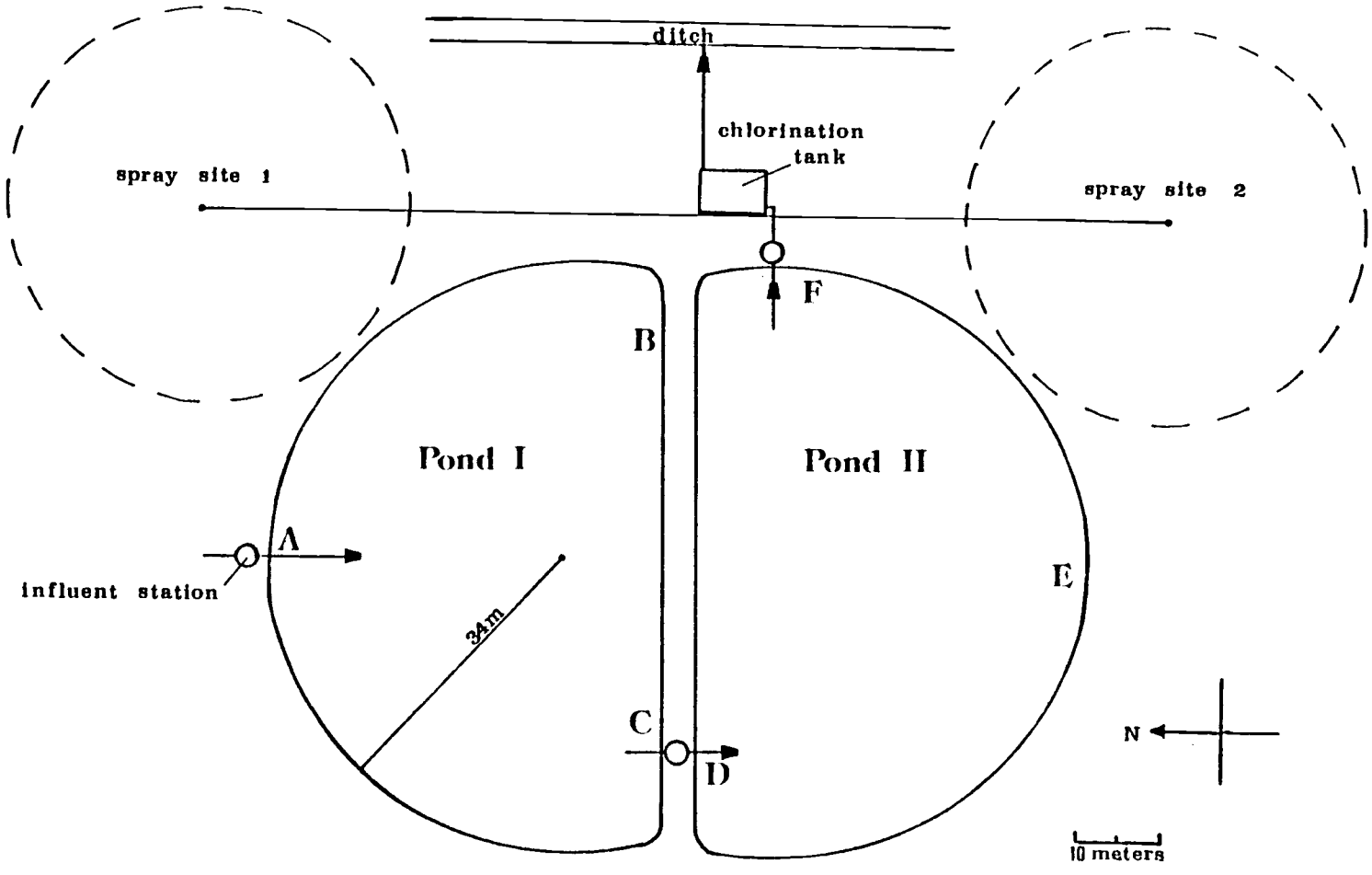


Figure 1. The Corvallis Airport Sewage Lagoon. The locations of stations A through F and the positions of the influent (at A) and the effluent (at F) are shown.

the sewage enters Pond II via a baffled culvert located between stations C and D. Treated sewage is pumped from the lagoon at station F into an 11 cubic meter concrete tank where it is chlorinated with 5.25% sodium hypochlorite for an average of one hour. The chlorinated effluent is discharged in winter into a ditch that flows into Dry Creek, then into the Willamette River at Booneville Slough. In summer, the chlorinated effluent is sprayed onto a hayfield next to the lagoon.

MATERIALS AND METHODS

Selection of Stations and Sampling Procedure

The selection of stations was based on a preliminary sampling of twelve sites around the perimeter of the lagoon during July and August of 1978. Water temperature, optical density (percent transmittance at 550 nm) and the relative abundance of phytoplankton species were recorded for these samples. The temperature was uniform within 2°C at all locations whereas the optical density varied considerably (29% to 95%) and so did the relative abundance of algal species. This patchy distribution of the phytoplankton in combination with time constraints led to a decision to sample three stations around the perimeter of each pond (Fig. 1).

Samples were collected weekly for two years from January 24, 1979 to January 8, 1981. Surface samples were dipped from the lagoon about two meters from the shore using a plastic bottle attached to a stick. Stations were always sampled sequentially, first station A and station F last. Before removing each 30 ml sample to a sterile bottle, the collection bottle was rinsed with lagoon water at that site. The six samples were stored and counted separately during the first year to estimate the variability between

stations. The second year, the three samples from each pond were mixed prior to counting.

Observations made on the day of sampling included: the air and water temperatures at station C, the amount of wind and estimated wind direction, cloud cover, precipitation, and the color of the lagoon water. Also noted were the previous week's weather, changes in the biota, and the presence of scum or bubbles in either pond (Appendix A).

Physical and Chemical Data

In addition to general climatic observations at the time of sampling, climatological data for the Corvallis area was obtained from the U.S.A. Weather Service's Climatological Records. These included air temperature, precipitation, evaporation and wind movement. The total incident radiation on a flat surface, measured with a Belfort Pyroheliograph, was also provided by the local Climatological Records data collection station.

Corvallis Wastewater Treatment Plant personnel monitored the sewage lagoon influent and effluent one day each month for biological oxygen demand (BOD), suspended solids (SS), and pH. The influent samples were a composite of samples collected over a 24-hour

period at station A before the sewage entered Pond I. The effluent samples were grab samples collected at station F from the outflow of Pond II at approximately midday. BOD, SS, and pH were determined according to the APHA Standard Methods for the Examination of Water and Wastewater.

Nutrients measured included phosphorus, nitrogen, carbon, and silica. For nutrient analysis, one liter samples of the surface water at station E were removed on six dates. The samples were stored in the dark at 10°C in cubitainers until filtration within 24 hours. One half of the sample was filtered through an 0.45 µm millipore filter. The filtered and unfiltered portions were preserved with a 40 mg/l final concentration of mercuric chloride and kept at 10°C until analysis with a Technicon Autoanalyzer II by the Corvallis EPA (U.S. EPA, 1979).

Enumeration of Algae

In the laboratory, each water sample was shaken and, depending on population density, a 10 to 100 ml. subsample was poured into a graduated cylinder. A few drops of 3% Lugol's solution was added to kill and fix the cells. Samples were sedimented for at least 3 hours, concentrated by siphoning off the supernatant, and the initial and final volumes recorded.

Quantitative counts were made of algal species according to the following procedure. A Palmer Cell was filled from a capillary pipet containing the well mixed, concentrated sample. The counting chamber was cleaned carefully to obtain an even distribution of cells. A Zeiss Standard Research microscope was fitted with a Whipple disc in the ocular for counting at 400x. A horizontal transect was counted until at least 100 cells were recorded. The total cells sometimes exceeded 100 to include all cells in the last square. The number of squares observed was used to determine the volume counted. The first year, the six samples were counted separately to estimate the variance between stations. The second year, 300 cells were counted in the composite sample from each pond to save time. Only those cells judged to be alive on the basis of possessing typical cytoplasmic morphology were counted.

The number of cells/ml was computed from the sample concentration factor and the volume counted as follows:

$$T \text{ (cells/ml)} = \frac{t\ (V_f/V_i)}{vs}$$

where: $v = \frac{aV}{A}$ = the volume covered by one small whipple square A at 400 X magnification in milliliters

and:
- a = area of one whipple square at 400 X
- V = Volume of the Palmer Cell (0.10 ml)
- A = Area of the Palmer Cell (250 mm^2)
- T = the number of cells/ml of each species
- t = the number of cells of each species counted in the sample
- s = the number of whipple squares counted
- V_f = the final sample volume after concentration
- V_i = the initial sample volume

The means and standard deviations of the counts of algal species in each pond were computed on the first year's samples only.

Enumeration of Parasites

The concentrated, preserved samples used for algal counts were reexamined to estimate the abundance of parasites in Pond II of the lagoon. A sample from one station (E if possible) each week in 1979 and the combined samples from 1980 were counted. On some dates samples had deteriorated so parasites could not be counted.

High magnification was necessary to resolve the minute parasites, so standard counting chambers could not be used to make direct quantitative counts. Instead, a thin water mount was examined with oil immersion at 1000 X magnification. The coverslip was sealed with immersion oil to prevent the mount from drying prematurely. Three replicate counts of 100 of the combined species of host cells were counted in successive transects. In samples where the number of parasitized host cells was very rare, three transects the width of the coverslip (22 mm) and height of the field were counted. Recorded were: the relative numbers of host cells of species that were known to be subject to parasitism in the lagoon; dead, parasitized host cells (those that contained an orange waste globule or had an empty parasite cyst attached, or partially digested cells); and encysted parasite zoospores. The cysts recorded included those with or without contents and those attached to both live and dead host cell walls.

The absolute abundance of the parasites was estimated from the relative counts by multiplying the fraction of cysts or lysed cells of each host times the previously determined absolute abundance of that host on the same date. The following equations summarize the calculations of parasite abundance.

$$C_a \text{ cells/ml} = \frac{C_r H_a}{H_r}$$

$$D_a \text{ cells/ml} = \frac{D_r H_a}{D_r + H_r}$$

where: C_a = absolute number of cysts
C_r = relative number of cysts on host cells
H_a = absolute number of host cells
H_r = relative number of host cells
D_a = absolute number of dead, parasitized hosts
D_r = relative number of dead, parasitized hosts

Occasionally, host species were observed in the relative abundance counts made under high magnification whose absolute abundance was not known because the species had not been encountered in the low magnification counts of the species of algae. In these instances, the absolute abundance of the alga was estimated from its abundance at high magnification relative to another algal species of known absolute abundance.

Taxonomy of the Algae and Parasites

Whenever new species of algae were encountered in the lagoon samples, they were identified in the following manner. Soon after collection, the water samples were mounted in a thin layer under a coverslip ringed with immersion oil. This procedure permitted observation of live cells at magnifications up to 1250 times.

Some of the dominant species were isolated in laboratory culture to facilitate taxonomic identification, electron microscopy, and study of the morphological variability. Isolation of 10 algal species was accomplished mechanically by streaking incubated, dilute lagoon samples on mineral medium. The algae were grown alternately on plates and in liquid media until contaminating organisms were eliminated. McLachlan's (1963) ASMG medium, minus the glycylglycine buffer, was used for isolation and maintenance of algal stocks.

Algae were generally identified to species. Exceptions were: a new species of Pteromonas, and some rarer taxa, e.g., Stigeoclonium, Mallomonas, and diatoms. Chlorella vulgaris, was identified according to the classification scheme of Fott and Nováková (1969). Taxonomically, the most difficult genus was Chlamydomonas because there are so many similar species described and certain critical taxonomic attributes (cell size and shape, thickness of cell wall) were variable in culture. For example, a strain of Chlamydomonas isolated in culture from the lagoon eventually contained both thick and thin walled cells. Another predominantly oval strain developed some larger, round cells in the same culture. Thus, the species names are

assigned only tentatively. The primary taxonomic resources were: Drouet (1968, 1978) and Drouet and Daily (1956) for the Cyanophyceae; G.M. Smith (1916, 1920, 1950), Tiffany (1934), Arce (1971), Komárek and Růžička (1969), Komárek and Ludvik (1971, 1972) and Trainor (1971) for the Chlorophyceae. Hustedt (1930) and Patrick and Reimer (1975) were used for identifying diatoms and Pringsheim (1956) for Euglena. Huber-Pestalozzi (1961) used for the Volvocales was supplemented with Ettl (1964, 1976) and Peterfi and Peterfi (1965) for Pteromonas and Chlamydomonas and Pringsheim (1969) for Chlorogonium.

Only three morphologically distinct parasites of algae were observed. The most common, Aphelidium chlorococcarum, was isolated and studied in two membered culture on Scenedesmus species. The taxonomy, life history and ultrastructure of this parasite are discussed in the section on Aphelidium. Another unidentified parasite (Chytrid Species 1) infected S. obliquus heavily during the fall of 1979 but was observed rarely during the remaining two year period. All parasites observed on Chlamydomonas resembled species of Rhizophydium, an epibiotic chytrid. The taxonomy of the latter two parasites was not investigated in detail. A cursory examination of Karling (1977) and Sparrow (1960) failed to reveal any organism

similar to Chytrid Species 1.

Culture and Ultrastructural Study of Aphelidium chlorococcarum

Aphelidium chlorococcarum was isolated from a lagoon sample collected November 4, 1979. The sample was filtered through a 3 µm nucleopore filter, and the filtrate containing zoospores of Aphelidium was added to Scenedesmus acuminatus isolated from the lagoon in ASMG medium. Tubes were incubated at 25°C and 150 footcandles in a 16 hour light/8 hour dark cycle. After 6 days, many of the S. acuminatus colonies were infected by A. chlorococcarum. The infected host cells were centrifuged at 1500 rpm for 10 minutes and centrifuged with sterile distilled water five times to reduce the bacterial contamination. The washed material was added to ASMG, incubated two days, and washed again on an 8 µm millipore filter with 0.5 liters of sterile distilled water. The washed filter containing infected host cells was placed in an axenic culture of Scenedesmus acuminatus in ASMG and incubated. Bacterial contamination during culture was kept at a minimum by repeated centrifugation and decanting. Other contaminating organisms were reduced by adding a small drop of the washed material to a culture of host cells growing in ASMG every 2-4 days. After a month, Aphelidium

chlorococcarum disappeared from the culture. Possibly the host cells in the ASMG medium were unable to support prolonged growth of the parasite. Another procedure which simulated the lagoon conditions more closely was used for isolation of A. chlorococcarum again in 1980. The culture medium was recently collected sewage lagoon water, filtered through an 0.45 µm millipore filter and autoclaved. To isolate Aphelidium, twelve potential host species were added to tubes of raw sewage containing A. chlorococcarum. Zoospores of Aphelidium were observed after 12 days in some of the Scenedesmus cultures. A small drop from these cultures was added to new cultures of Scenedesmus in sterile sewage. Encysted zoospores of Aphelidium were abundant in three of the cultures after 5 days (Scenedesmus armatus, Scenedesmus obliquus, and a culture collection strain, S. obliquus UT72). Contamination was reduced as before. These cultures were maintained for several months until the end of the study.

The ultrastructure of strains of Aphelidium from both culture periods was studied. The electron microscope fixation procedures differed in 1979 and in 1980. In 1979 material from a mixture of cultures of Aphelidium chlorococcarum on Scenedesmus acuminatus at several stages of infection were fixed in the following

manner. Samples were concentrated by centrifugation and decanting, then fixed in 3% gluteraldehyde in 0.1M Sorenson's Buffer (pH 7) for 6 hours. The fixed sample was embedded in 2% ion agar and washed in buffer overnight. One percent OsO_4 was added to the sample in buffer for 4 hours and the sample then was dehydrated for 15 minutes each in increasing concentrations of acetone. The sample was infiltrated in Spurr's medium in a 1:2 plastic:acetone mixture for 16 hours followed by a 2:1 plastic:acetone solution for 8 hours, then transferred to fresh plastic with catalyst and cured overnight at 70°C.

In 1980, A. chlorococcarum on other Scenedesmus species was fixed as described by Gauriloff et al. (1980). OsO_4 was added to the gluteraldehyde to give a final concentration in the sample of 0.05% OsO_4 and 1% gluteraldehyde. It was then infiltrated for 30 minutes, decanted and embedded in agar. The remainder of the procedure was as described above.

Sections were cut with a diamond knife on a Porter-Blum MT2 ultra microtome. Section thickness was 400-700 A°. Sections were poststained with Reynolds (1963) lead citrate and examined in a Philips EM 300 transmission electron microscope at 60 kV accelerating potential. Images were recorded on Kodak 4489 film.

RESULTS

The following results include climatological data and selected physical and chemical data from the sewage lagoon. The abundance of the phytoplankton in both ponds and the abundance of the parasites of algal species in Pond II will also be presented.

Physical and Chemical Data

Climatic Data

Each year, solar radiation varied from approximately 100 langleys per day in December to 500 langleys per day in July. There was more light during May and June of 1979 and September of 1980 than in the corresponding months of the alternate year; otherwise curves each year were similar (Fig. 2). The temperature values for the two years were also nearly identical. Minimum monthly mean temperatures occurred in January (0 - 4^{o}C). January of 1979 was the coldest of the three Januaries. Each year, the maximum monthly mean temperature (19^{o}C) was observed in July. The summer of 1979 was warmer than that of 1980.

Precipitation fluctuated more than the other climatic variables both from month to month and from year to year (Fig. 2). The driest months were June and July (1979) and July and August (1980). December (1980) was

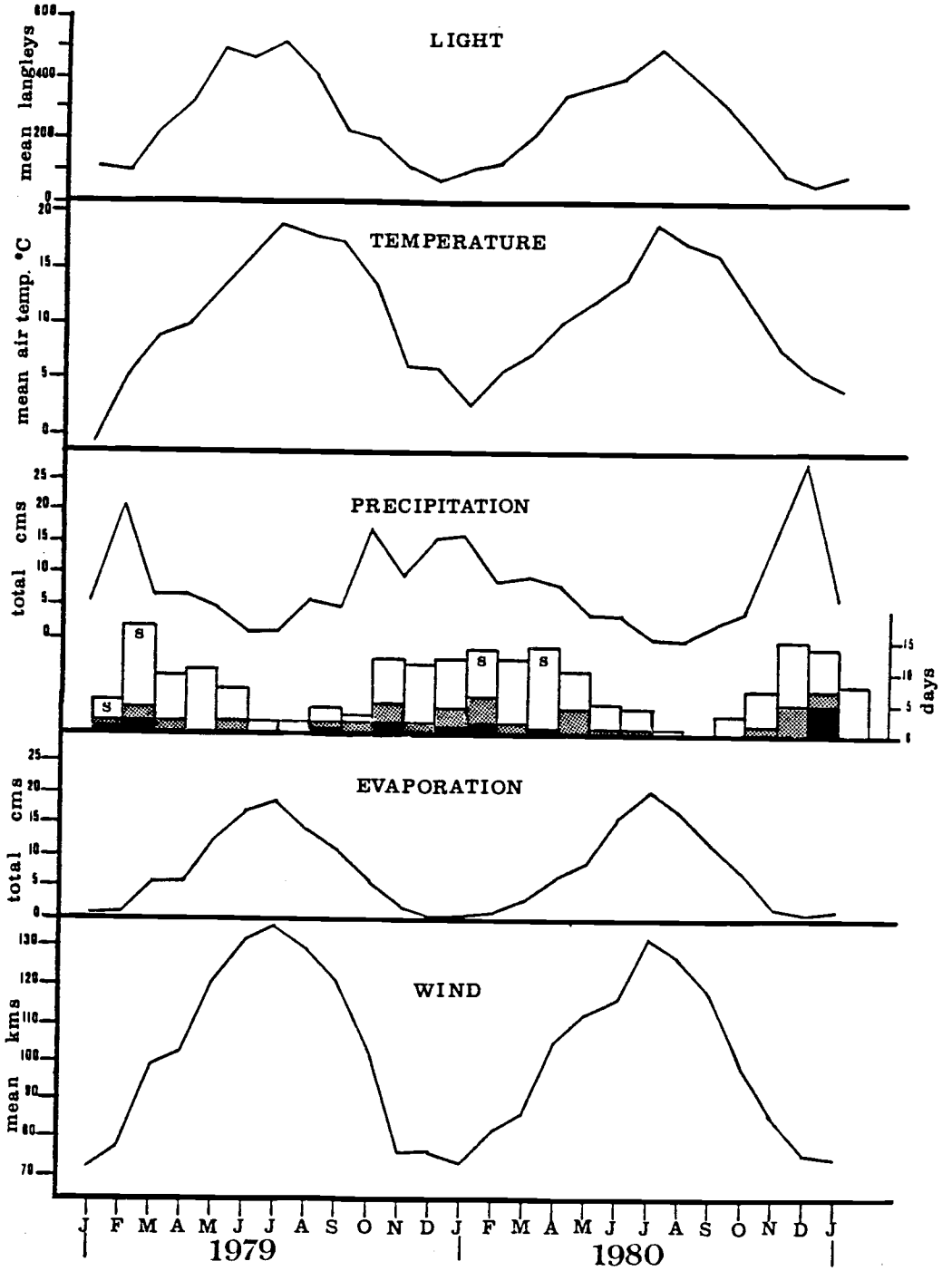


Figure 2. Climatic data for 1979 and 1980 at Corvallis, Oregon. Precipitation and evaporation are expressed as total cm/month whereas light, temperature and wind are the means of daily totals. The precipitation histogram indicates the number of days each month where precipitation exceeded 0.25 cms (white), 1.25 cms (stipled), or 2.54 cms per day (black). An "s" means that measurable snowfall occurred during the month.

the wettest month of the study period. Precipitation exceeded 0.2 cm/day on more days in February, 1979 than in any other month. Measurable amounts of snow accumulated during January and February of 1979 and in January and March of 1980. On January 30, 1980, sampling was prevented by thick ice on the lagoon which was covered with 2 cm of snow. Also, thinner ice was present on the lagoon at the end of January 1979, and for a week in early December, 1980 (Appendix A). Evaporation and wind were highly correlated and closely related to the other climatic variables as expected. The maximum evaporation and wind occurred in July and the minimum in December. Evaporation was generally slightly lower from July of 1979 to July of 1980 than in the corresponding months of the other year. There was more wind movement in 1979 than in 1980.

In summary: light, temperature, evaporation, and wind were positively correlated with each other while precipitation was negatively correlated with these factors. While there were small differences between the years, there is a striking similarity in the overall pattern each year. From January to July, the light, temperature, wind and evaporation increased and precipitation decreased. From July to January the pattern was reversed. Light and evaporation were the

lowest in December while temperature and wind minima were in January. Precipitation was high in October, as well as in December and January during the exceptionally wet winter of 1979/80. In 1980, the same pattern occurred except that precipitation was lowest in July and August and highest in December.

Sewage Lagoon Influent and Effluent: Selected Measurements

The pH of the influent varied from 6.4 to 8.8 while the effluent values ranged from 7.0 to 9.0 and were generally slightly higher than those of the influent on the same dates (Figs. 3 and 4). Seasonal changes in the pH ofthe influent sewage were observed; maxima were in early summer and fall while minima were in late summer and winter. The lowest values occurred in the winter of 1979. In the effluent, the pH was highest in the summer and lowest in the winter except for high pH values observed early in 1979. Also, in the effluent, the pH in the fall of 1979 was lower than in the same period the following year.

The effluent had lower BOD values (2 to 23 mg/l) than the influent (19 to 263 mg/l) (Figs. 3 and 4). Seasonal fluctuations were not evident in either the influent or the effluent BOD. The first year, the BOD of the influent sewage was higher and more variable

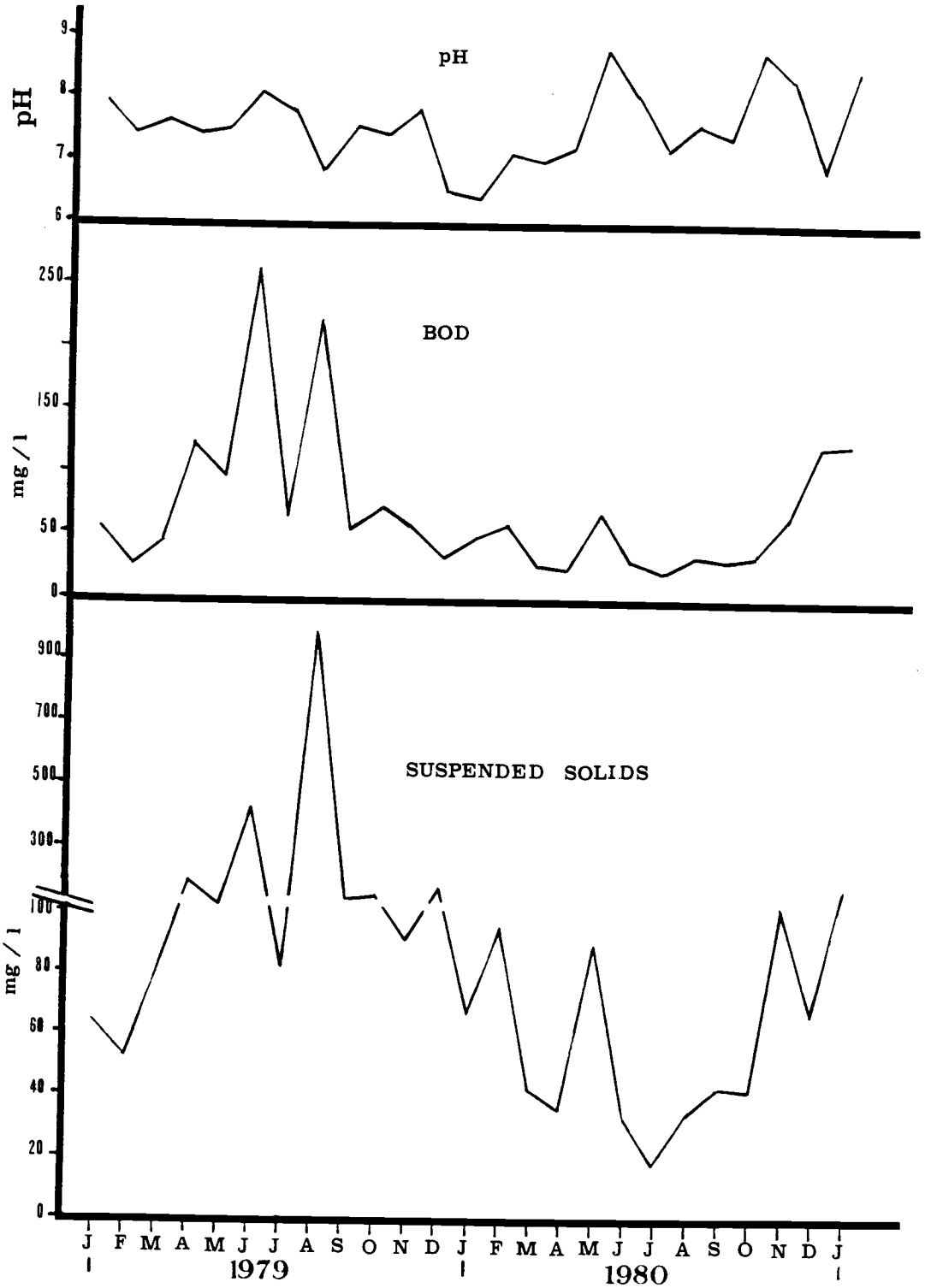


Figure 3. Influent to Pond I. Monthly values of the pH, BOD, and suspended solids during 1979 and 1980.

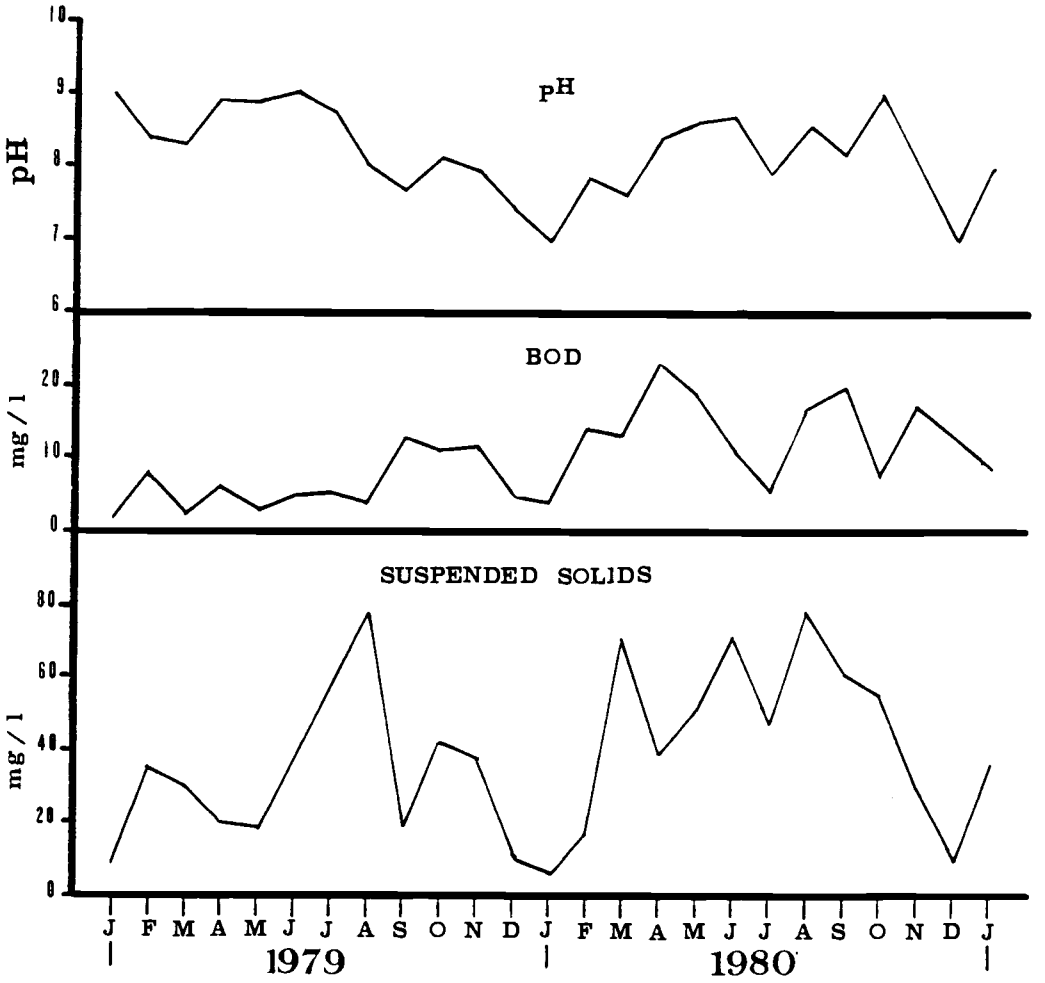


Figure 4. Effluent from Pond II. Monthly values of the pH, BOD, and suspended solids during 1979 and 1980.

than the second year, while the reverse was true of the effluent BOD.

Enormous fluctuations in the suspended solids occurred in the influent (18 to 987 mg/l) (Fig. 3). The highest values (those above 200 mg/l) were found the first summer and the lowest during the second summer. The effluent suspended solids values ranged from 6 to 78 mg/l and were generally lower than that of the influent (Fig. 4). The highest values typically occurred in the summer, particularly during the second year. On the average, 70% of the suspended solids and the BOD present in the influent waste water were removed by the lagoon system.

In summary, the measured parameters fluctuated widely from month to month. They did not cycle annually or seasonally, and they did not correlate with one another. An exception to this is the close relationship between the influent BOD and the suspended solids.

Nutrient Concentrations in Pond II

The concentrations of selected major nutrients in Pond II during part of 1980 are summarized in Figure 5. The total phosphorus varied from 2.8 mg/l at the end of July to 1.1 mg/l in October. In July, most of the phosphorus existed as particulate phosphorus, but by

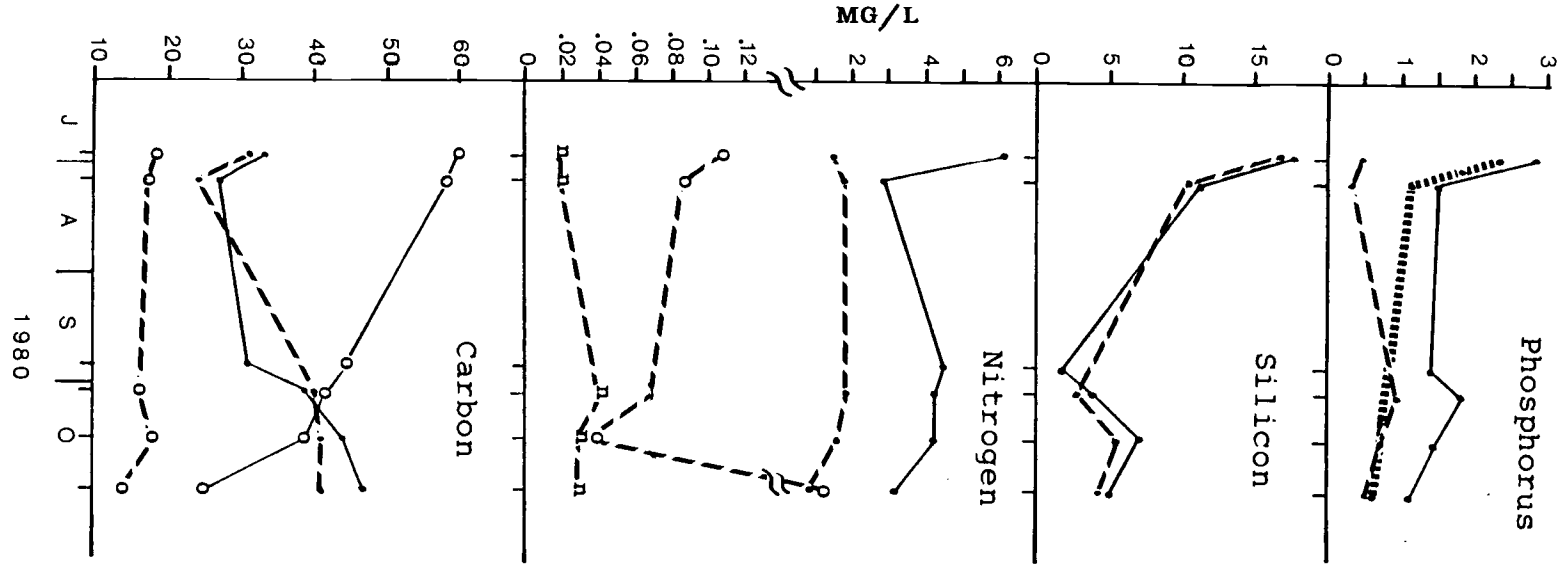


Figure 5. The concentrations of major nutrients in Pond II from July to October, 1980. The forms of phosphorus shown are: ——— total phosphorus, ... total particulate phosphorus, and — — — soluble phosphorus. The forms of silicon are: ——— total silicon, and -·-·-·- dissolved silicon. Nitrogen curves are: ——— total organic nitrogen, -·-·- dissolved organic nitrogen, o— — —o ammonium ion, and n— — —n nitrate and nitrite. The forms of carbon are: o———o total organic carbon, o— — —o dissolved organic carbon, ——— total inorganic carbon; and — — — dissolved inorganic carbon.

fall, the phosphorus in the particulate and soluble fractions were approximately equal. Soluble phosphorus was 0.3 to 0.9 mg/l in Pond II. Total silica declined from 17.6 mg/l in July to 1.5 mg/l in late September. Most of this silica was dissolved silica. Total organic carbon (mostly as particulate carbon) was more concentrated in the summer (60 mg/l), but this decreased to 25 mg/l by the end of October, 1980. Dissolved inorganic carbon increased from July to October and ranged from 24 to 41 mg/l. Organic nitrogen was the most common fraction of total nitrogen (3 - 6 mg/l), followed by ammonium ion (0.04 - 0.11 mg/l) and combined nitrate and nitrite (0.02 - 0.04 mg/l).

Abundance of Algae

Total Phytoplankton

Annual cycles of the total phytoplankton abundance closely paralleled seasonal changes, increasing as temperature and illumination rose (Fig. 6). Both ponds were more productive in the summer of 1980 than in 1979. Phytoplankton abundance in the two ponds of the lagoon was remarkably similar in most months. In general, Pond II had slightly more cells/ml than Pond I, although in the summer this tendency sometimes was reversed. Phytoplankton abundance varied from $2x10^2$ to

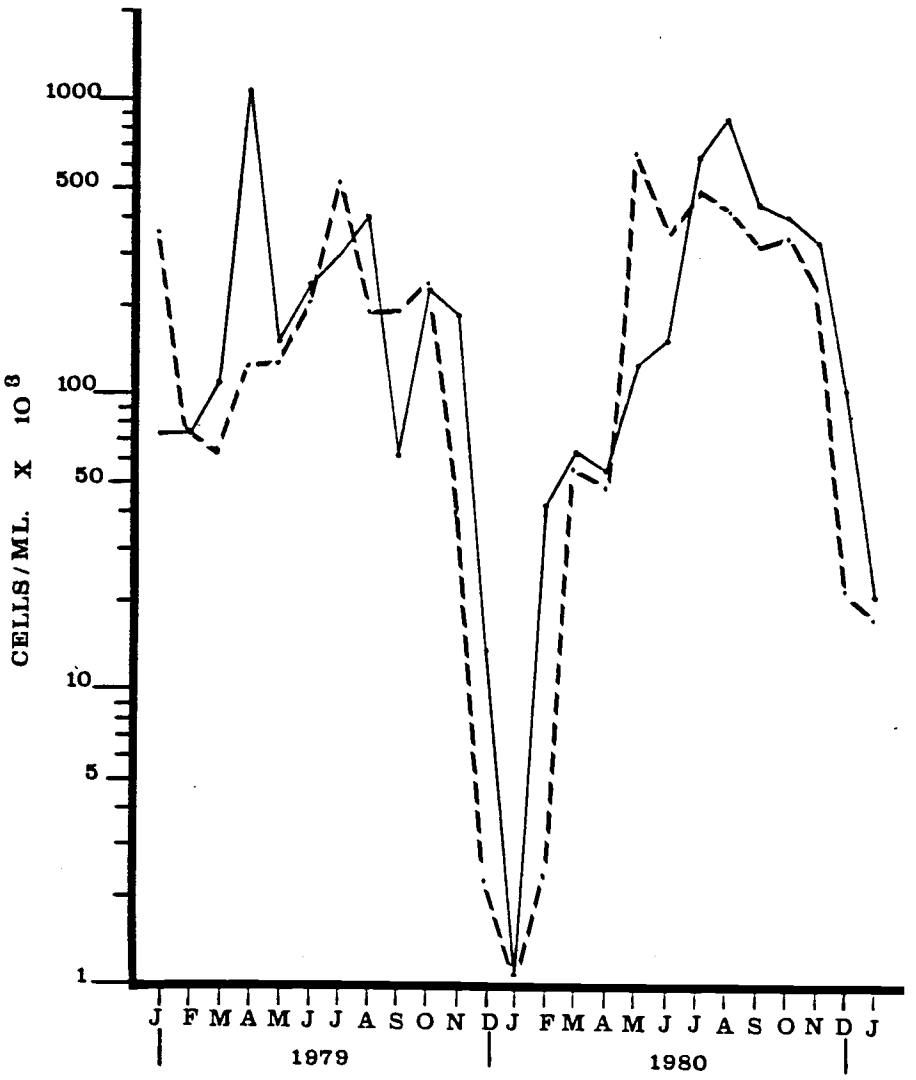


Figure 6. Abundance of the total phytoplankton. The mean monthly abundance of all phytoplankton expressed as the cells/ml on a logarithmic scale is shown for Pond I — — , and for Pond II ———.

$1x10^6$ cells/ml and averaged $3x10^5$ cells/ml from spring through fall in the lagoon. Both years, the largest number of cells occurred during July in Pond I and August in Pond II. The fewest cells occurred in January. Relatively large values of phytoplankton abundance in Pond I for January 91979) and May (1980) and in Pond II for April (1979) corresponded to clumps of Chlorella vulgaris which were counted in the sample. Because this species is one of the smallest of the phytoplankton, large numbers do not represent a correspondingly large biomass. Furthermore, the greater error in counts of organisms such as Chlorella that occur as large clumps of cells may result in an inaccurate estimate of phytoplankton abundance.

Succession

The curves of abundance of individual species in the lagoon tended to form an overlapping continuum so that dominance by one cluster of species was gradually replaced by other species. Consequently, there was not a clear demarcation between groups of species as the seasons changed. Furthermore, the successional patterns of species varied each year and were different in the two ponds (Figs. 7 and 8, and Tables 1 and 2). Many, if not all, species were present in the lagoon

Table 1. Pond I. The dominant species of phytoplankton are ranked in order of relative abundance. The most abundant species each month is indicated by a "1", the second most abundant species by a "2", etc. Dominant species are those with a mean monthly abundance greater than $(10)^4$ cells/ml except in months when the phytoplankton density was low. Species with densities below $(10)^4$ cells/ml are indicated by parentheses around the rank number.

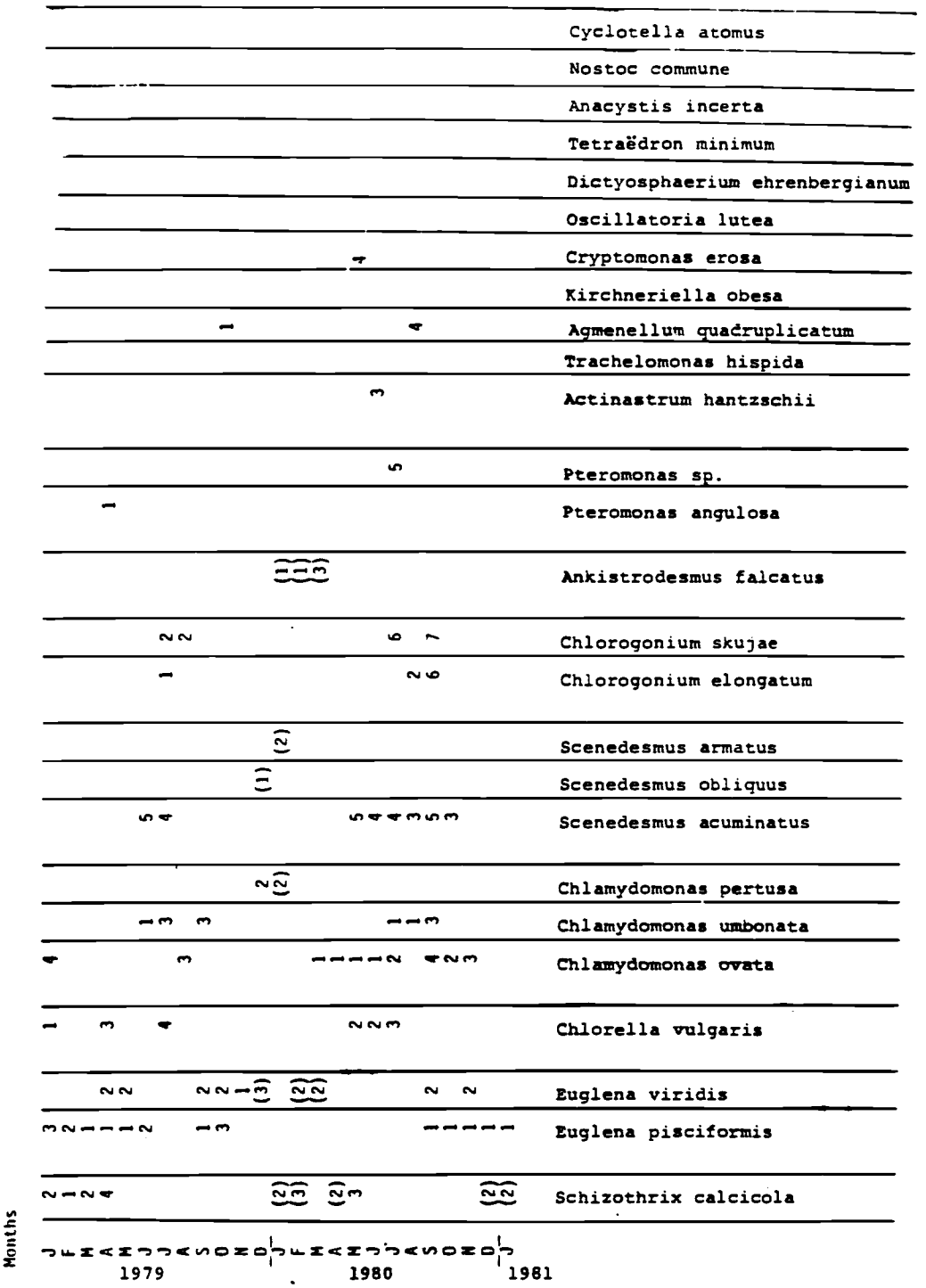


Table 2. Pond 11. The dominant species of phytoplankton are ranked in order of relative abundance. The most abundant species each month is indicated by a "1", the second most abundant species by a "2", etc. Dominant species are those with a mean monthly abundance greater than $(10)^4$ cells/ml except in months when the phytoplankton density was low. Species with densities below $(10)^4$ cells/ml are indicated by parentheses around the rank number.

Months	Cyclotella atomus	Nostoc commune	Anacystis incerta	Tetraëdron minimum	Dictyosphaerium ehrenbergianum	Oscillatoria lutea	Cryptomonas erosa	Kirchneriella obesa	Agmenellum quadruplicatum	Trachelomonas hispida	Actinastrum hantzschii	Pteromonas sp.	Pteromonas angulosa	Ankistrodesmus falcatus	Chlorogonium skujae	Chlorogonium elongatum	Scenedesmus armatus	Scenedesmus obliquus	Scenedesmus acuminatus	Chlamydomonas pertusa	Chlamydomonas umbonata	Chlamydomonas ovata	Chlorella vulgaris	Euglena viridis	Euglena pisciformis	Schizothrix calcicola
J																						3			2	(4)
F																						1			1	1
M																				3	(5)	4	1	(2)		
A																					1		2	3		
M												(3)						6	2		1	5	2				
J											8	7					1	1	6		1	6	5				
A										(3)		2					1	3	1			4	2				
S																	1	4	3			2	5				
O																	1	1	6			5	4				
N																	1	1	4			8	4				
D																	1	1	1			4	4				
J																	(1)	(1)	3			2	5				
F																	(1)	(1)	2			5	4				
M														(2)			(3)		6	2		1	5				
A														(4)					4	(3)		1	4				
M															4				1	(2)		1	3				
J																			1	(2)		1	3				
A																			1	(3)		1	3				
S																			2	(2)		1	3				
O																			2	(4)		1	3				
N																			2			1	3				
D																			2			1	3				
J																			2			1	3				
F																			2			1	3				
M																			2			1	3				
A																			2			1	3				
M																			2			1	3				
J																			2			1	3				
A																			2			1	3				
S																			2			1	3				
O																			2			1	3				
N																			2			1	3				
D																			2			1	3				
J																			2			1	3				

1979 1980 1981

all year, but they were sometimes so rare that they were overlooked (Appendix B). Following is a discussion of the seasonal changes of associated species, the autecology of selected taxa in each ond and a comparison of the two ponds.

Pond I: Seasonal Assemblages of Species

In Pond I, the phytoplankton community was dominated by an assemblage of *Euglena* species in the cooler months alternating in the warmer months with an assemblage of *Chlamydomonas* and *Chlorogonium* species (Fig. 7, Table 1 and Appendix B). The "winter" assemblage, characteristic from September until spring included, in addition to two species of *Euglena*; *Schizothrix calcicola*, present both years from December to February, and *Ankistrodesmus falcatus* in the winter of 1980. This cool weather assemblage was followed by a "summer" assemblage in June of 1979, and in March of 1980. Taxa dominant in the "summer" assemblage were *Chlamydomonas* species, *Chlorogonium* species and *Scenedesmus acuminatus*. In addition, *Pteromonas angulosa* was abundant in August of 1979, and *Chlorella vulgaris* in the spring of 1980.

Pond II: Seasonal Assemblages of Species

In Pond II, three distinct seasonal assemblages were observed (Figure 8, Table 2 and Appendix B). A *Euglena* assemblage in the winter was followed in the spring by a *Chlamydomonas* - *Chlorella* assemblage. This was replaced in the late summer and fall by a diverse assemblage dominated by *Scenedesmus* species. The *Euglena* assemblage appeared in October and ended in May of 1979, and in March of 1980. In addition to two *Euglena* species, the assemblage sometimes included *Schizothrix calcicola* and *Ankistrodesmus falcatus*. Because the fall *Scenedesmus* assemblage tended to persist until January, and the spring *Chlamydomonas* species often appeared in February, these overlapped with the *Euglena* assemblage. The spring assemblage consisted primarily of *Chlamydomonas ovata*, which was dominant sporadically from January through November. At times, this was associated with other *Chlamydomonas* species, *Chlorella vulgaris*, *Kirchneriella obesa* and (in 1979 only) *Pteromonas* sp. The summer and fall phytoplankton were the most diverse of the assemblages. From July through September of 1979 and June through October of 1980, the *Scenedesmus* species assemblage overlapped with the *Chlamydomonas* species assemblage. Together with *Scenedesmus*, many other taxa were

abundant at times. These included: Chlorella vulgaris, Tetraëdron minimum, Cyclotella atomus, Dictyosphaerium ehrenbergianum, Kirchneriella obesa, Oscillatoria lutea, and Nostoc commune.

Ponds I and II Compared

During the winter and spring, the species composition of the ponds was similar. In the winter, Euglena species were dominant in both ponds, although they were abundant longer in Pond I than in Pond II. Schizothrix and Ankistrodesmus were associated with Euglena in both ponds. The warm month assemblage of Pond I was dominated by Chlamydomonas species and Scenedesmus acuminatus which were also present in Pond II in the spring and fall. Pond I had up to ten times the number of Chlamydomonas cells, and more cells of Chlorogonium than Pond II.

The ponds differed most during the summer and fall. At this time, several Scenedesmus species were very abundant in Pond II, while in Pond I only Scenedesmus acuminatus was prominent for any length of time, and it was never the most abundant species. In Pond II, Scenedesmus species were prominent for several months each summer. Other genera which were much more abundant in Pond II were: Kirchneriella, Oscillatoria, Tetraëdron, Nostoc, Cyclotella, and Chlorella.

Autecology

Scenedesmus species were present in both ponds throughout the year, but were much more abundant in Pond II than in Pond I. In both ponds, they were rare from January through March, then generally increased to a maximum in mid-summer, declined in September and rose to a second, smaller maximum in the fall. In Pond I, the only abundant species of Scenedesmus was S. acuminatus. It was most abundant in late July of 1979 and in 1980 from July through September (Fig. 7 and Appendix B). In Pond II, the S. acuminatus maximum occurred in July and August of both years (Figs. 8 and 11). Each year, after the summer maximum, a secondary maximum occurred in October. The combined counts of S. armatus, S. abundans, and S. quadricauda were most abundant from July through November of 1980 in Pond II. None of these species (all were designated S. armatus because they were indistinguishable during counting) were very common in Pond I.

The Euglena species were most abundant during the cooler months, although they were present at lower abundances during most of the two-year study period (Figs. 7 and 8). Both species were abundant for a longer period in Pond I. In Pond I, Euglena pisciformis reached maxima in January, from March through May

of 1979, and in the early fall of both years. In Pond II, E. pisciformis followed a similar pattern except that it was rare in the fall of 1979. Euglena viridis populations were considerably more common in Pond I where maxima were in the spring and fall. In Pond II, E. viridis was seldom abundant.

In contrast to Euglena, Chlamydomonas species occurred most commonly in the warmer months. Peak populations of Chlamydomonas ovata occurred periodically from March through November in both ponds over the two year period. The other two Chlamydomonas species were observed less frequently. C. umbonata became very abundant during the early summer in both ponds. Chlamydomonas pertusa was rare in Pond I. In Pond II, it was most abundant in April and November of 1979, and also was common from March through May of 1980.

Several species were characteristically abundant during a particular season. Schizothrix calcicola, a small, filamentous blue-green was found more often in Pond I and in the cooler months. In Pond I, it was prominent in the winter (January through April of 1979) and was also abundant in the spring of 1980. In Pond II, it was most abundant in the winter of 1979 and in July of 1980. Chlorella vulgaris was most numerous in the spring each year in both ponds and also in July of

1980. The Chlorogonium species were present in both ponds in the warmer months, but were considerably more abundant in Pond I. The population of Chlorogonium elongatum in Pond I reached a peak in July of 1979 and in August of 1980. In Pond II it was most abundant in July of both years, although the numbers were much lower than in Pond I. Chlorogonium skujae was abundant in the late summer in Pond I and in Pond II in June of 1979.

Most species were present in both ponds of the lagoon, but some were considerably more abundant in only one of the ponds (Figs. 7 and 8). In Pond I, these included Schizothrix calcicola, Euglena species, and Chlorogonium elongatum. In Pond II, uniquely abundant species were: Trachelomonas hispida, Oscillatoria lutea, Scenedesmus obliquus, S. armatus, Cyclotella atomus, Kirchneriella obesa, and Tetraëdron minimum. In the late summer of 1980, Pond II also supported a more abundant growth of the blue-greens: Nostoc commune, Anacystis incerta, and Oscillatoria lutea. Diatoms were rare in the lagoon but Cyclotella atomus became abundant in Pond II at the same time as the blue-greens.

Only a few species had a similar pattern of abundance both years: Scenedesmus acuminatus, S. obliquus,

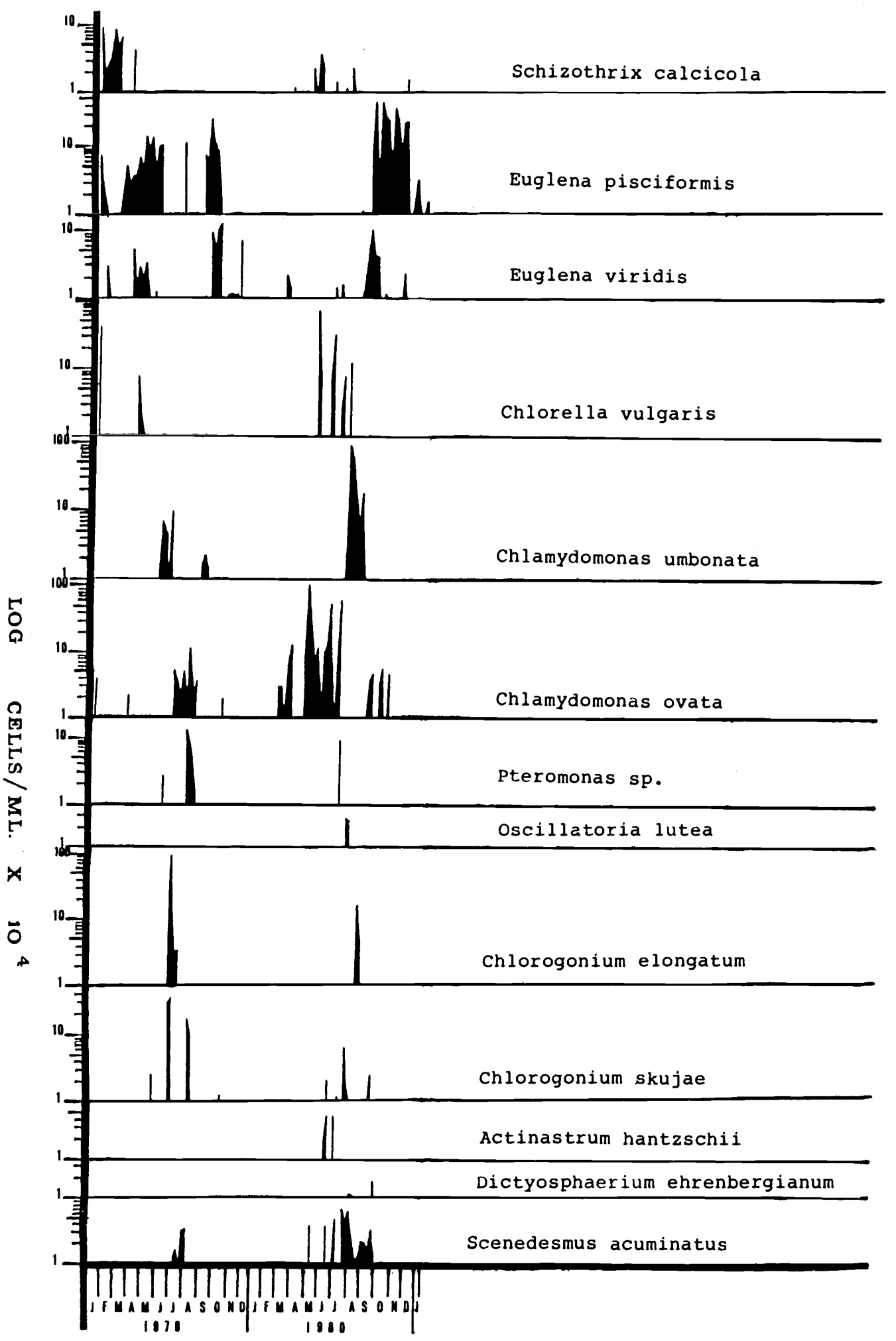


Figure 7. Dominant species of phytoplankton in Pond I of the sewage lagoon. Values are expressed as the logarithm of the number of cells/ml. Only values in excess of 10^4 cells/ml are shown.

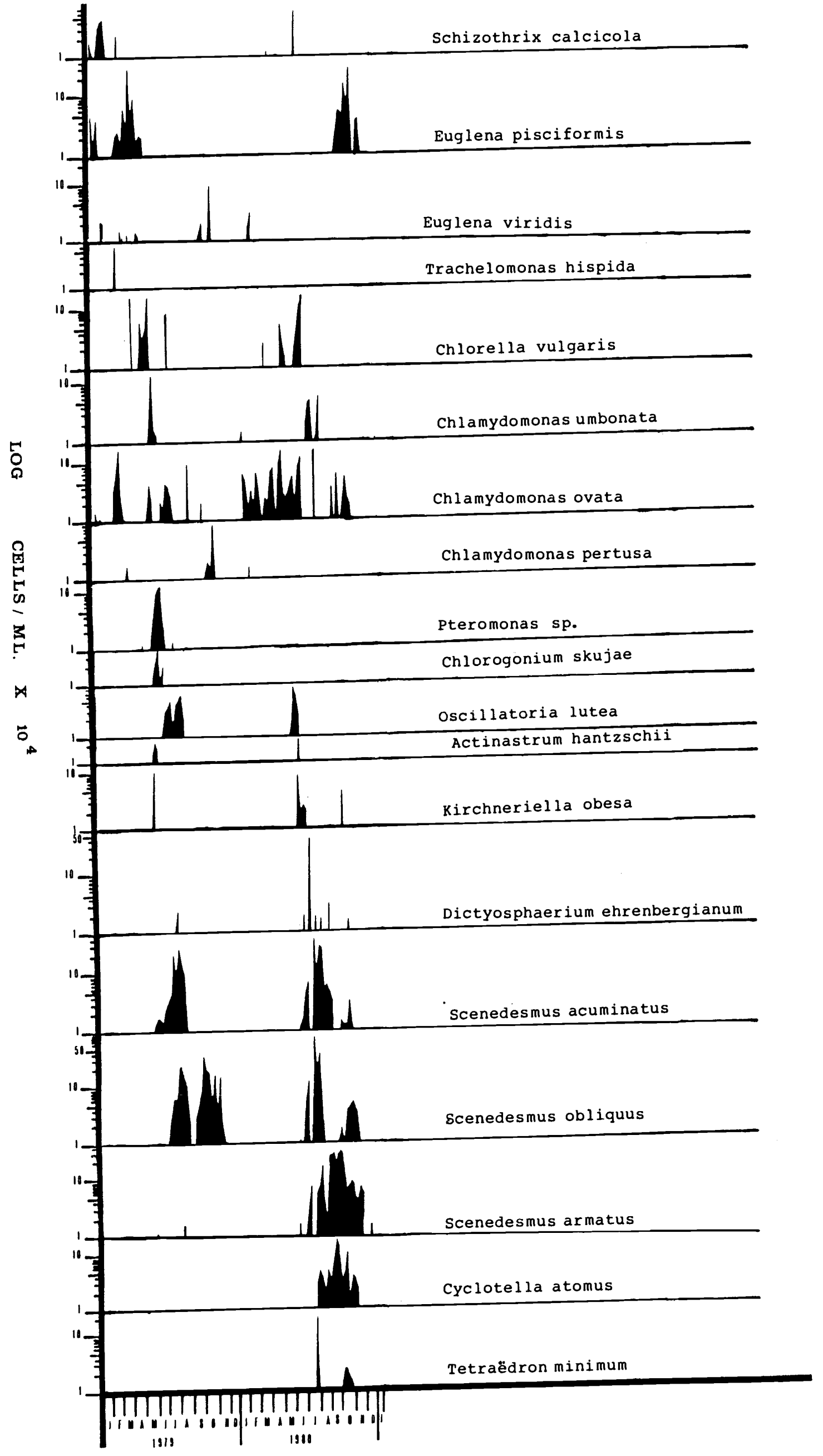


Figure 8. Dominant species of phytoplankton in Pond II of the sewage lagoon. Values are expressed as the logarithm of the number of cells/ml. Only values in excess of 10^4 cells/ml are shown.

Chlorella vulgaris, Oscillatoria lutea. Kirchneriella obesa and Actinastrum hantzschii.

Abundance of Parasites

Only three morphologically distinct parasites were observed on algae in Pond II, two chytrids and Aphelidium chlorococcarum. Of the 35 most abundant species of algae in the lagoon, 14 were parasitized (Table 3). These are all members of the Chlorophyta. An unidentified parasite, designed Chytrid Species 1, only infected Scenedesmus obliquus. Chlamydomonas species (Volvocales) were parasitized by Rhizophydium sp. Parasite strains resembling Aphelidium chlorococcarum infected 9 species in the Chlorococcales, 3 culture collection strains of Scenedesmus (Chlorococcales), and 2 Pteromonas species (Volvocales). Preliminary cross inoculation experiments of Aphelidium chlorococcarum strains on different host species in culture suggested that there is more than one strain of the parasite. Also the rate of infection varied on different host species. Infection was fastest on Scenedesmus acuminatus.

The periodicity of the more abundant parasites and their hosts are discussed below. The host species are organized according to the taxonomic system of Smith (1950).

Table 3. Host range of parasites from the sewage lagoon. Algae from the lagoon are classified according to G.M. Smith (1950). (L) = the parasite was observed on this host in the lagoon, (C) = the parasite was grown in culture on this host, and (-) = no parasites were observed on this host. The parasites are abbreviated "A" for Aphelidium chloroccarum, "R" for Rhizophydium sp., and "C" for Chytrid Species 1.

Parasites			Algae
A	R	C	
			Chlorophyta
			Volvocales
-	-	-	*Chlorogonium elongatum* Dang.
-	-	-	*Chlorogonium skujae* Peterfi
-	L	-	*Chlamydomonas umbonata* Pascher
-	L	-	*Chlamydomonas ovata* Dang.
-	L	-	*Chlamydomonas pertusa* Chod.
L	-	-	*Pteromonas angulosa* Lemm.
L	-	-	*Pteromonas* sp.
			Tetrasporales
-	-	-	*Sphaerocystis schroeteri* Chod.
			Ulotrichales
-	-	-	*Sticchococcus chodati* (Bail.) Heering
			Chlorococcales
L	-	-	*Golenkinia radiata* (Chod.) Willie
L	-	-	*Dictyosphaerium ehrenbergianum* Naegeli
LC	-	-	*Ankistrodesmus falcatus* (Corda) Ralfs
L	-	-	*Tetraëdron minimum* (A. Braun) Hansgirg
-	-	-	*Chlorella vulgaris* Beijerinck
L	-	-	*Kirchneriella obesa* v. *major* (Bernard) Smith
L	-	-	*Actinastrum hantzschii* Lagerheim
LC	-	-	*Scenedesmus acuminatus* (Lag.) Chod.
LC	-	-	*Scenedesmus armatus* (Chod.) Smith
LC	-	L	*Scenedesmus obliquus* (Turp.) Kutzing.
C	-	-	*Scenedesmus obliquus* D3 Univ. of Texas Culture Collection UT393
C	-	-	*Scenedesmus obliquus* (Pringsheim strain) Univ. of Texas Culture Collection UT72
C	-	-	*Scenedesmus brasiliensis* Bohlin Univ. of Texas Culture Collection UT79
			Euglenophyta
-	-	-	*Euglena pisciformis* Klebs
-	-	-	*Euglena viridis* Ehr.
-	-	-	*Phacus turgidulus* Pochmann
-	-	-	*Trachelomonas hispida* (Perty) Stein emend. Deflandre
			Chrysophyta
-	-	-	*Mallomonas* sp.
-	-	-	*Cyclotella atomus* Hust.
-	-	-	*Gomphonema olivaceum* v. *calcarea* Cleve
-	-	-	*Navicula* sp.
-	-	-	*Nitzschia* sp.
			Uncertain affinity — Cryptophyceae
-	-	-	*Cryptomonas erosa* Ehr.
-	-	-	*Cryptomonas* sp.
			Cyanophyta
-	-	-	*Agmenellum quadruplicatum* Bréb.
-	-	-	*Anacystis incerta* D. & D.
-	-	-	*Schizothrix calcicola* (Agardh) Gomont
-	-	-	*Oscillatoria lutea* Agardh
-	-	-	*Nostoc commune* Vauch.

Individual Parasites

Order: Chlorococcales
Family: Scenedesmaceae

Scenedesmus obliquus

Scenedesmus obliquus was abundant each year from June until December (Fig. 9). Two maxima were separated by a decline in September. In 1979, the maxima occurred in August (244,000 cells/ml) and October (363,000 cells/ml), and in 1980 they were in July (808,000 cells/ml) and October (53,000 cells/ml).

S. obliquus was infected by two parasites, Aphelidium chlorococcarum and Chytrid Species 1. The most frequently observed stage in the life histories of these parasites, the encysted zoospore, is morphologically identical in both species. Consequently, the two parasites were counted as one. For the most part, the parasite counts refer to Aphelidium chlorococcarum except for the period from October to December of 1979 when the stages that distinguish Chytrid Species 1 were abundant.

The first appearance of parasites in 1979 coincided with the beginning of the annual increase of S. obliquus in June (Fig. 9). At that time, encysted zoospores of Aphelidium chlorococcarum were observed on 26% of the live S. obliquus cells. Judging by the

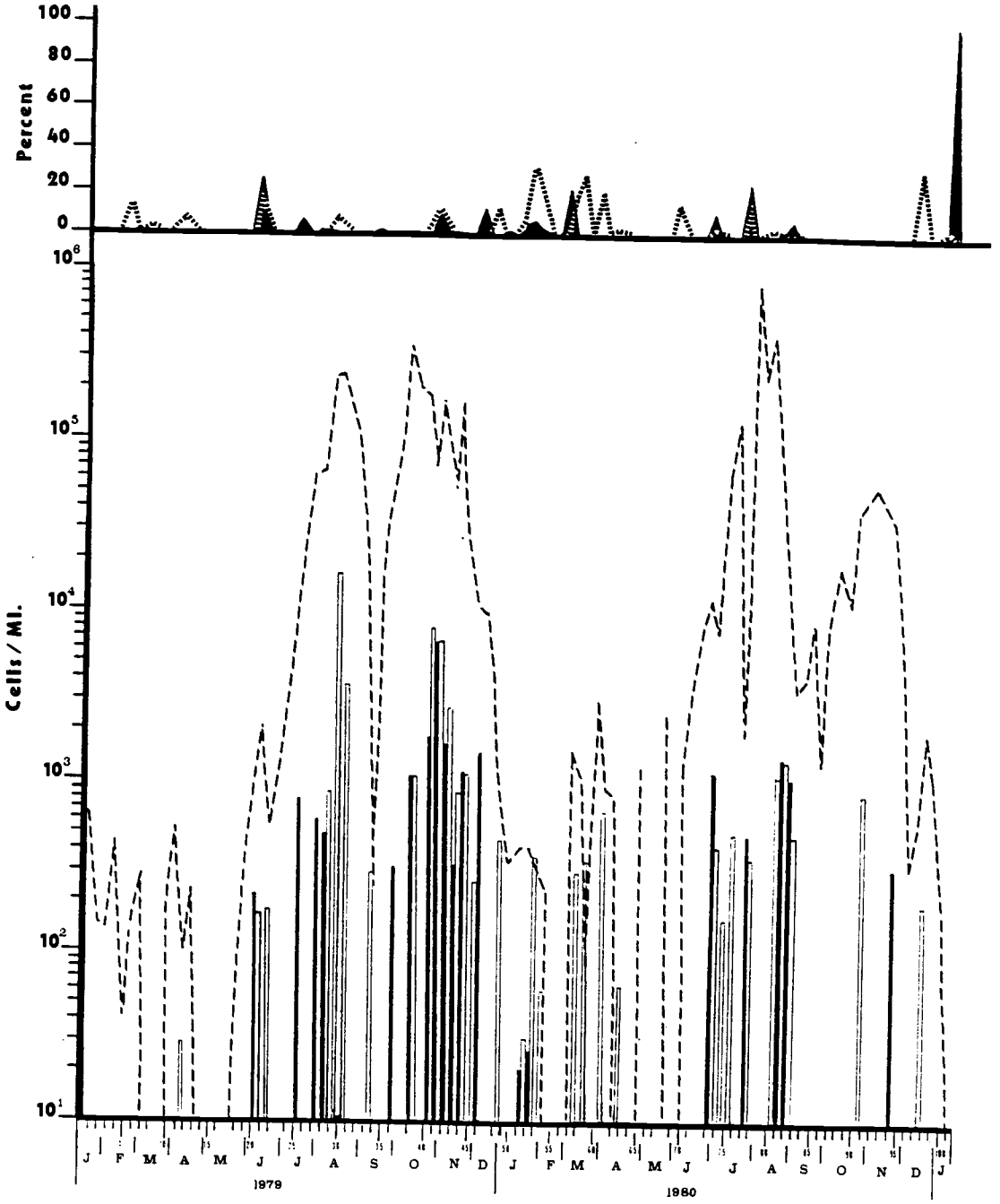


Figure 9. The abundance of Scenedesmus obliquus and its parasites: Aphelidium chlorococcarum and Chytrid Species 1. The lower graph shows the number of: host cells/ml each week .▬▬▬., infected host cells (black bar), and dead host cells (white bar) plotted on a logarithmic scale. In the upper graph are the percentages of infected (solid) and dead (▮▮▮▮▮) host cells. Missing data for parasite abundance is indicated by deletion of the tick mark for that week on the horizontal axis.

presence of orange globules in the dead cells, 20% of the host population was killed by parasitism. This was the most severe infestation observed on S. obliquus, yet the host population continued to increase for two weeks before it declined from approximately 2000 cells/ml to 600 cells/ml. However, no parasite zoospores or dead host cells were observed on the day of the minimum. Evidently this episode of parasitism had little effect on the population of S. obliquus.

Parasites were rare during the remainder of the summer maximum of S. obliquus (Fig. 9). In July, up to 8% of the host cells were parasitized but the population continued to increase rapidly. From the August maximum of S. obliquus until the decline in September, no zoospores of parasites were observed although dead, parasitized S. obliquus cells were present. Apparently the decline of S. obliquus in September was unrelated to parasitism.

Both Aphelidium chlorococcarum and Chytrid Species 1 were observed parasitizing low fractions of the host population during the fall of 1979. Although parasite zoospores and dead host cells occurred in every sample in October and November, the percentage of infected cells was low. During the increase in the S. obliquus population, fewer than 1% of the cells were infected.

More severe parasitism occurred three weeks after the October maximum of S. obliquus. As the host population declined, higher infection rates (9% and 13%) and more dead cells were observed. Parasitism and winter weather both seem to have contributed to the decline of S. obliquus.

Again, in 1980, severe parasitism of S. obliquus occurred primarily during the summer. Before the July maximum, zoospores of Aphelidium chlorococcarum were observed on two dates. In late June, three weeks after the S. obliquus increase began, 11% of the cells were infected. A small decline in the host population occurred during the following week, then the population continued to increase. Parasite zoospores were not observed again for three weeks, but about 1% of the host cells were dead during this interval. Four weeks after the first appearance of zoospores, they reappeared on 25% of the host cells one week before the host maximum. The same week, 19% of the S. obliquus population was dead, and the number of live cells fell from 130,000 cells/ml to 1900 cells/ml. However, the decline was brief; the S. obliquus population rose to its maximum for the two year period (800,000 cells/ml) the following week. After the host maximum, less than 8% of the S. obliquus cells were parasitized during

August. Although S. obliquus was abundant in the fall, parasitism was rare.

Order: Chlorococcales
Family: Scenedesmaceae

Scenedesmus armatus and related species

As mentioned previously, S. armatus, S. abundans and S. quadricauda were often indistinguishable, so the counts of these were combined. For brevity, the three will be arbitrarily termed S. armatus. S. armatus was considerably less abundant in 1979 than the following year (Fig. 10). The cell density was highest from March through October, 1979, with the greatest number of cells (16,000 cells/ml) occurring in August. No S. armatus cells were observed in September of 1979. In 1980, S. armatus was abundant from March through December. The annual increase began in June and culminated in a maximum of 411,000 cells/ml in October followed by a gradual decline through January of 1981.

In 1979, Aphelidium chlorococcarum zoospores and dead cells of S. armatus were common from April through July (Fig. 10). The highest percentages of infected S. armatus cells were observed in April (33%), May (20%), June (17%) and July (74%). Each of these episodes of parasitism was associated with a decrease in the number

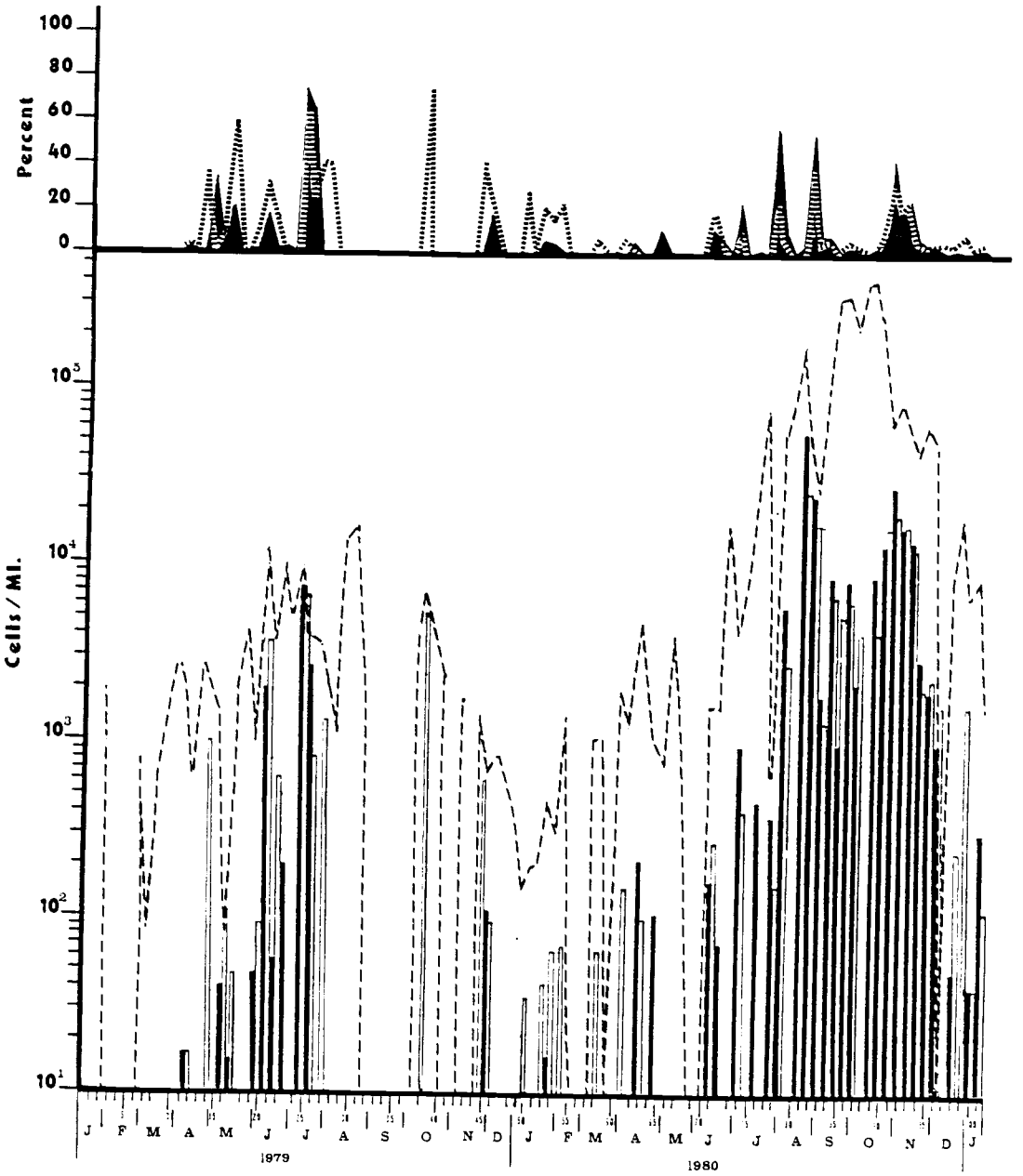


Figure 10. The abundance of Scenedesmus armatus and its parasite, Aphelidium chlorococcarum. The lower graph shows the number of: host cells/ml each week .-.-., infected host cells (black bar), and dead host cells (white bar) plotted on a logarithmic scale. In the upper graph are the percentages of infected (solid) and dead (▪▪▪▪▪▪▪) host cells. Missing data for parasite abundance is indicated by deletion of the tick mark for that week on the horizontal axis.

of live cells and an increase in the fraction of dead S. armatus cells.

Severe infections were observed in April (33%) and two weeks later in May (20%). The population of S. armatus declined somewhat during this interval. However, 58% of the population had been killed by parasitism by the date of the May infection, so it is possible that parasitism reduced the population density of S. armatus. By June, 17% of the population was infected and 31% killed by parasitism. On the same date, the host population was substantially greater than it had been the previous week. During the week following the 17% infection, the host population fell again and so did the fraction of infected cells. The relationship of these fluctuations to parasitism is unclear.

In July, 74% and 65% of the S. armatus population was infected on successive weeks. The density of the host population decreased from a maximum of 9500 cells/ml when 74% of the population was parasitized to several thousand cells/ml for the next four weeks. Throughout the decline, large fractions of dead cells occurred (23% to 64%). Two weeks after the last dead cells were observed, the host population resumed growth. While the amount of the decline of S. armatus in July is small, the facts that the decline lasted for

a month, and large fractions of dead cells occurred suggest that this episode of parasitism had a considerable impact on S. armatus.

In 1980, Aphelidium chlorococcarum was observed parasitizing S. armatus in most samples from June through December. The most severe infections occurred when the host was relatively abundant in June (22%), July (56%), August (54%) and October (42%). Greater numbers of dead S. armatus cells and declines in the number of live host cells were associated with each of these events.

By June (1980), when 22% of the S. armatus cells were parasitized, 10% were dead and the host population was lower. The S. armatus population increased rapidly until another episode of severe parasitism (56%) occurred in July. A substantial decline in the S. armatus population was observed the same week and 23% of the host cells were dead. Severe parasitism (greater than 10%) continued into August when in one sample 54% of the population was parasitized and 37% were dead. The S. armatus population increased rapidly despite this episode of severe parasitism from July to August, then decreased substantially on the date of the 54% infection.

After this, low levels of parasitism accompanied dense populations of S. armatus until two weeks after the October maximum. The number of host cells fell substantially when 42% of the population was infected. Severe infections persisted on at least 19% of the host cells for two more weeks and 20% of the cells were dead. But after the initial decline of S. armatus in October, the host population density remained constant (about 50,000 cells/ml) until December, when winter began.

Order: Chlorococcales
Family: Scenedesmaceae

Scenedesmus acuminatus

The main period of abundance of S. acuminatus from June to December of 1979 included two maxima: one in early August (290,000 cells/ml) and another at the beginning of November (10,000 cells/ml). There were two S. acuminatus maxima again in 1980. The largest (415,000 cells/ml) was at the end of July, and a smaller peak (35,000 cells/ml) occurred in October.

In 1979, low fractions (5%) of the S. acuminatus population were parasitized by A. chlorococcarum from June through August (Fig. 11). After the S. acuminatus maximum in August, zoospores disappeared, but dead host cells were present in every sample (up to 12%) as the

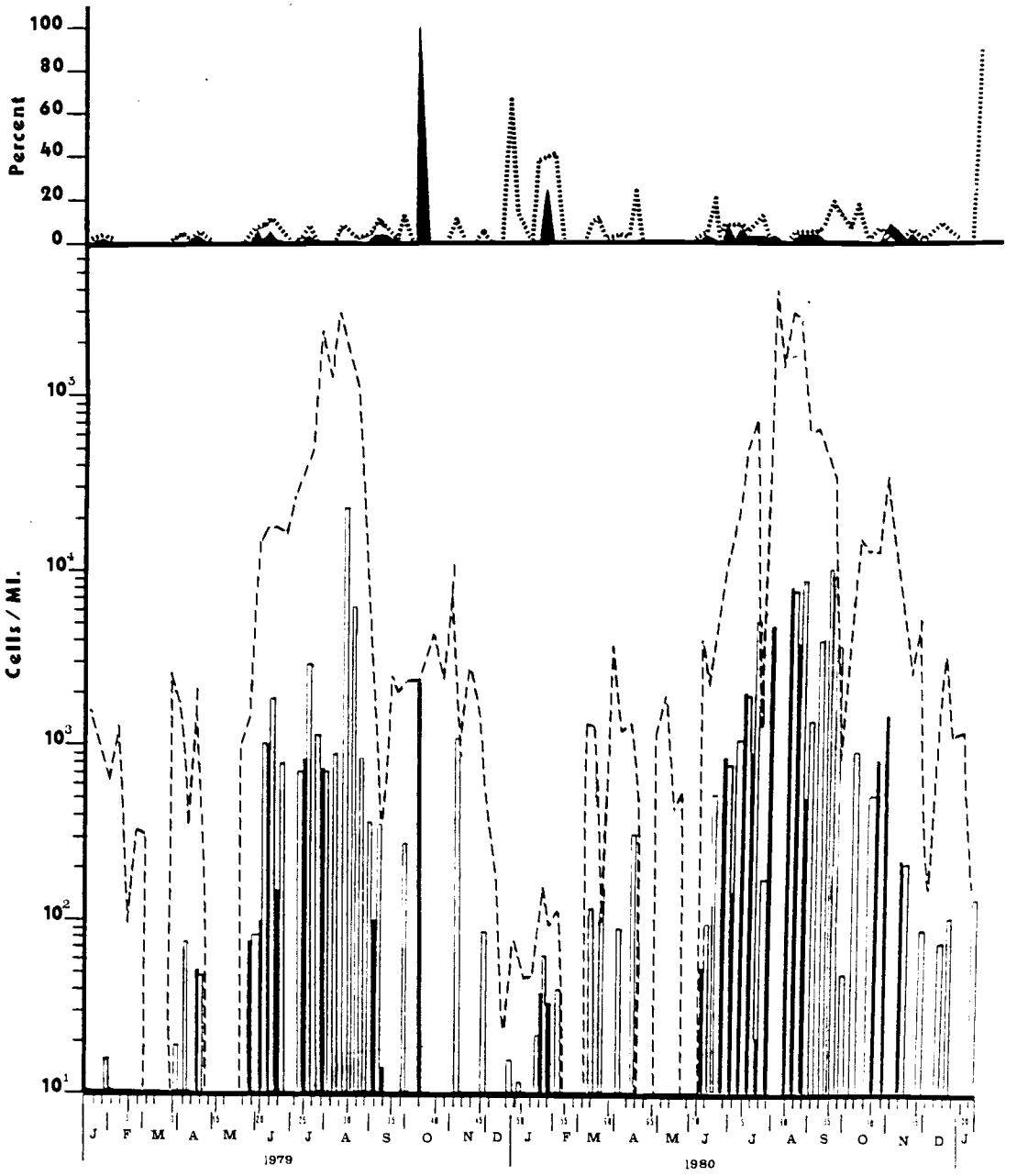


Figure 11. The abundance of Scenedesmus acuminatus and its parasite, Aphelidium chlorococcarum. The lower graph shows the number of: host cells/ml each week .▬▬▬., infected host cells (black bar), and dead host cells (white bar) plotted on a logarithmic scale. In the upper graph are the percentages of infected (solid) and dead (▮▮▮▮▮▮) host cells. Missing data for parasite abundance is indicated by deletion of the tick mark for that week on the horizontal axis.

host declined to a September minimum. During the fall increase in S. acuminatus, there was little evidence of parasitism and A. chlorococcarum zoospores were observed only once, in October.

In 1980, as in the year before, A. chlorococcarum zoospores occurred in most samples during the summer as S. acuminatus increased, but less than 7% of the cells were infected. As S. acuminatus declined, zoospores were not observed. However, up to 20% of the population consisted of dead, parasitized cells. In the fall, near the October maximum of S. acuminatus, 6% of the cells were again infected by A. chlorococcarum zoospores.

Order: Chlorococcales
Family: Scenedesmaceae

Actinastrum hantzschii

Actinastrum, unlike most of the other species of phytoplankton in the lagoon, was abundant mainly for one month each year; from June to mid-July. In 1979, the maximum was 22,000 cells/ml and in 1980 it was 26,000 cells/ml.

Parasitized cells of Actinastrum and encysted zoospores resembling Aphelidium chlorococcarum were seen during maximum populations of Actinastrum

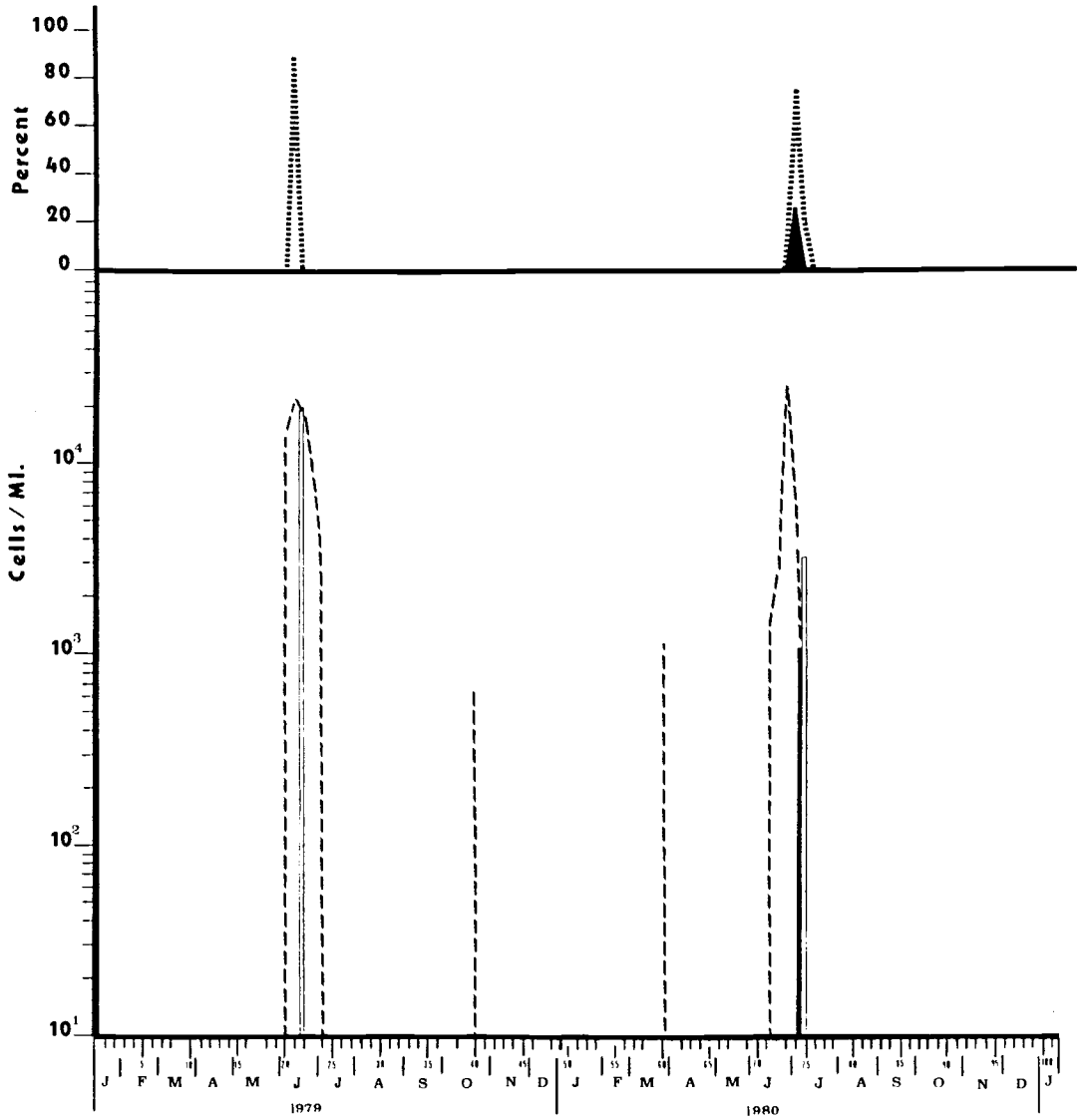


Figure 12. The abundance of Actinastrum hantzschii and its parasite, Aphelidium chlorococcarum. The lower graph shows the number of: host cells/ml each week .-▬-., infected host cells (black bar), and dead host cells (white bar) plotted on a logarithmic scale. In the upper graph are the percentages of infected (solid) and dead (▮▮▮▮▮▮▮) host cells. Missing data for parasite abundance is indicated by deletion of the tick mark for that week on the horizontal axis.

hantzschii. Brief periods of severe parasitism occurred each year (Fig. 12). In 1979, on the day the population of Actinastrum reached its maximum, 87% of the cells were dead, but no zoospores of the parasite were observed. In 1980, one week following the maximum population of Actinastrum, 74% of the host cells were dead and zoospores of Aphelidium were abundant (25%). By the following week live cells of Actinastrum had decreased to below detectable levels and remained so for the rest of the year.

Order: Chlorococcales
Family: Oőcystaceae

Ankistrodesmus falcatus

Ankistrodesmus was observed throughout the two year study period but was most abundant during the summers. Each year, the highest numbers occurred in July. In 1979 there were 6600 cells/ml, and in 1980 the maximum was 19,000 cells/ml.

Ankistrodesmus was parasitized by an organism whose encysted zoospores and orange waste globules resembled those of Aphelidium chlorococcarum. During 1979, less than 7% of the Ankistrodesmus population was parasitized (Fig. 13). Zoospores occurred on only three dates, each time during a peak population of Ankistrodesmus.

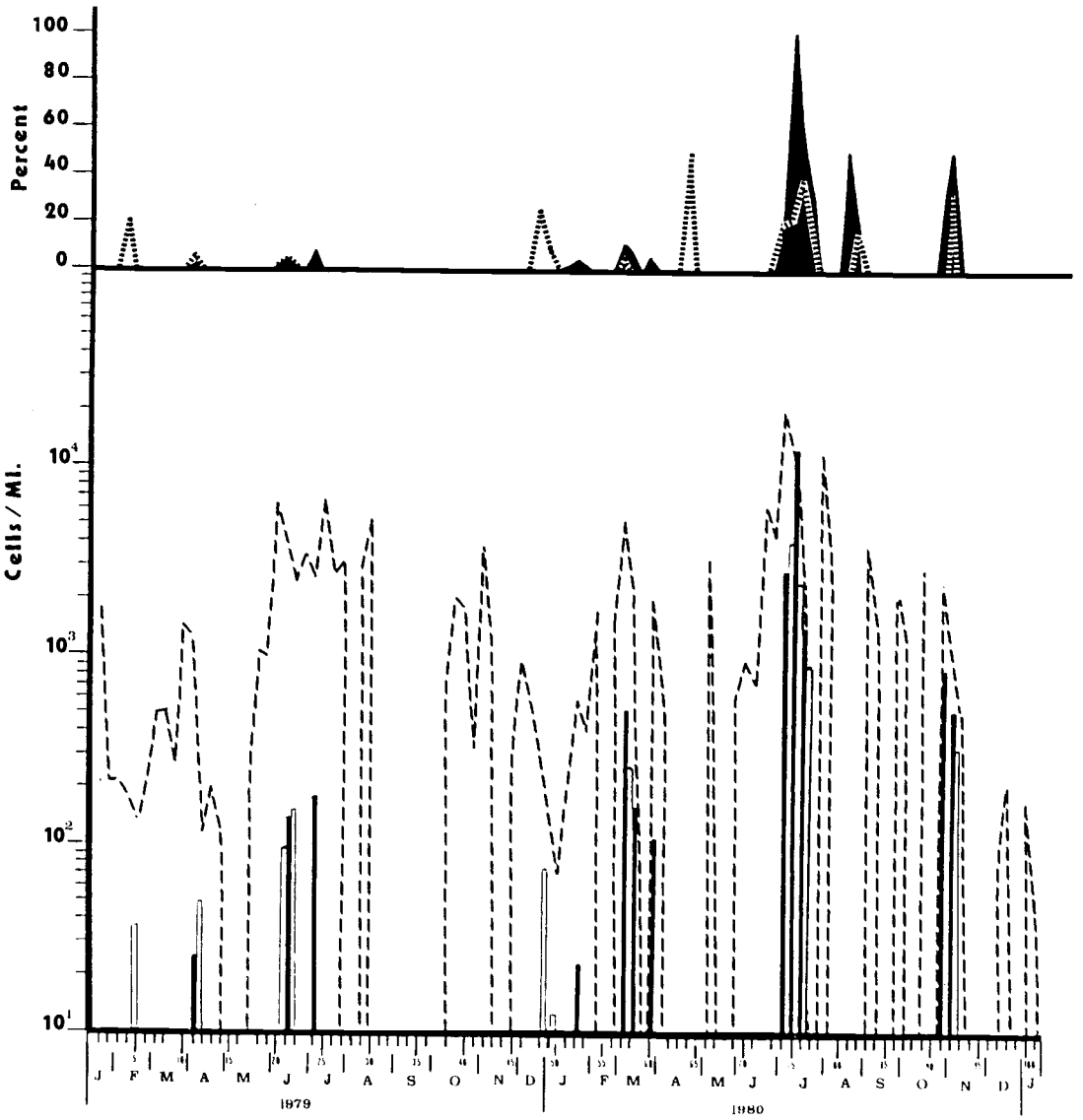


Figure 13. The abundance of Ankistrodesmus falcatus and its parasite, Aphelidium chlorococcarum. The lower graph shows the number of: host cells/ml each week .▬▬▬., infected host cells (black bar), and dead host cells (white bar) plotted on a logarithmic scale. In the upper graph are the percentages of infected (solid) and dead (▮▮▮▮▮▮▮) host cells. Missing data for parasite abundance is indicated by deletion of the tick mark for that week on the horizontal axis.

In 1980, episodes of severe parasitism occurred in July (100%), August (50%) and October (50%). Apheli-dium zoospores were rarely observed until the date of the Ankistrodesmus maximum in July when 14% of the cells were infected. A week after the maximum, 100% of the Ankistrodesmus cells had zoospores attached and thereafter the host population declined rapidly to zero in August. During this period, dead cells varied from 20-37% of the host population. As many as 50% of Ankistrodesmus cells were parasitized even after the live Ankistrodesmus cells had become very rare. Although the decline of Ankistrodesmus was not substantial, parasitism is strongly implicated in this decline. The period of infection in October (50%) lasted two weeks and 33% of the Ankistrodesmus cells were dead. A small decline of the host population occurred.

Order: Chlorococcales
Family: Oöcystaceae

Tetraëdron minimum

Tetraëdron was rare in 1979. In 1980, it was present from May through January, 1981, with host maxima in July (121,000 cells/ml) and in October (23,000 cells/ml).

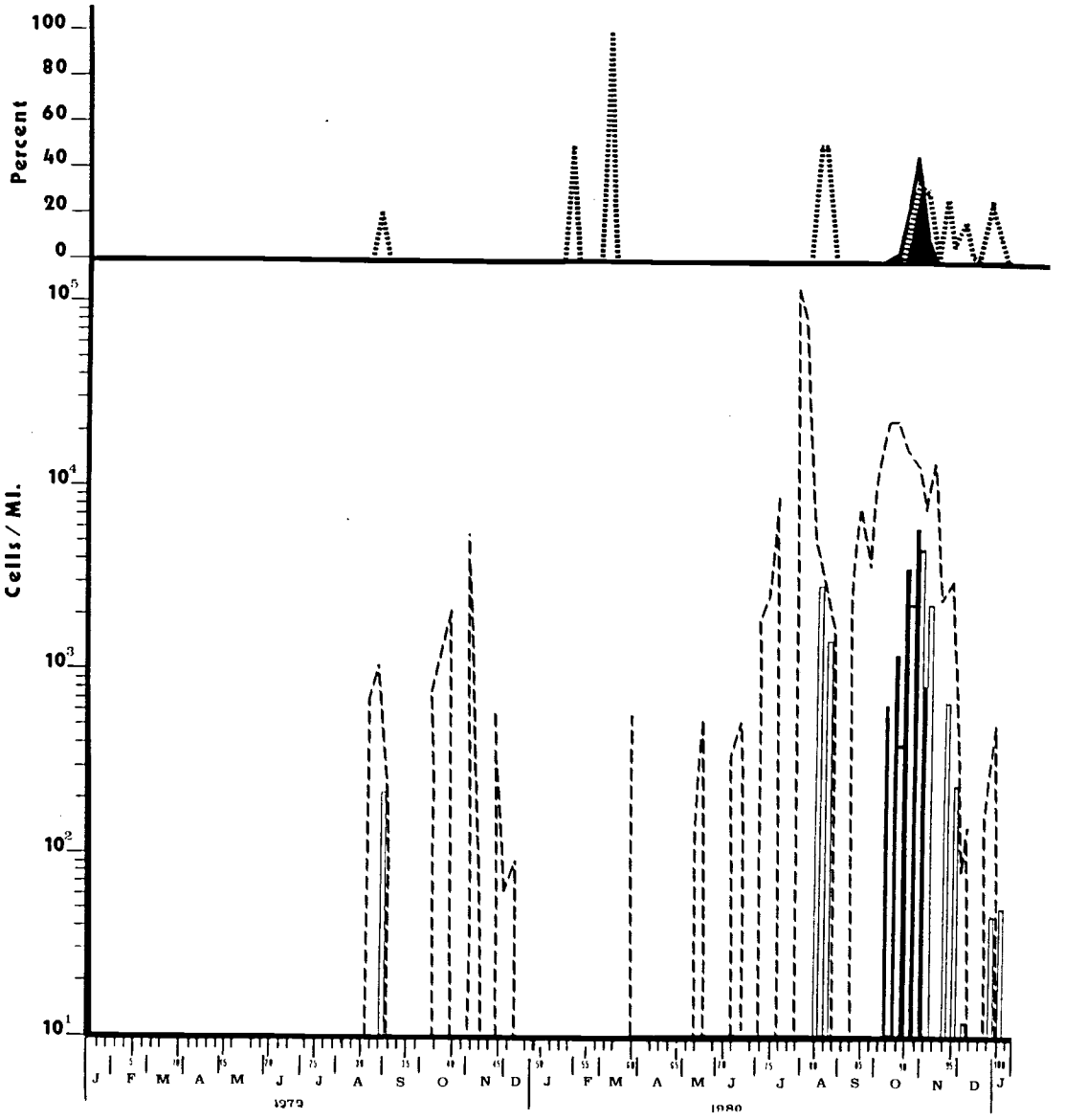


Figure 14. The abundance of Tetraëdron minimum and its parasite, Aphelidium chlorococcarum. The lower graph shows the number of: host cells/ml each week ▬▬▬, infected host cells (black bar), and dead host cells (white bar) plotted on a logarithmic scale. In the upper graph are the percentages of infected (solid) and dead (▮▮▮▮▮▮▮) host cells. Missing data for parasite abundance is indicated by deletion of the tick mark for that week on the horizontal axis.

The parasite observed on Tetraëdron resembled Aphelidium chlorococcarum. Zoospores of Aphelidium were not observed in 1979 (Fig. 14). In 1980, after the Tetraëdron summer maximum, 50% of the population was dead as the host declined, but no Aphelidium zoospores were observed. In October, Aphelidium zoospores infected 46% of the Tetraëdron population and up to 35% of the cells were killed by the parasites. Tetraëdron declined rapidly after the infection.

Order: Chlorococcales
Family: Dictyosphaeriaceae

Dictyosphaerium ehrenbergianum

Dictyosphaerium was absent in 1979 except for two weeks in August. From July 1980 until January of 1981, the population density was approximately 30,000 cells/ml.

In 1979, a few dead host cells suggested parasite activity, but no zoospores were observed (Fig. 15). An episode of severe parasitism by an organism resembling Aphelidium chlorococcarum occurred in July of 1980 when Dictyosphaerium was increasing. Encysted zoospores infected 100% of the Dictyosphaerium population and 76% of the host cells were dead. Dictyosphaerium continued to be relatively abundant the rest of the year and free of infection except on one occasion.

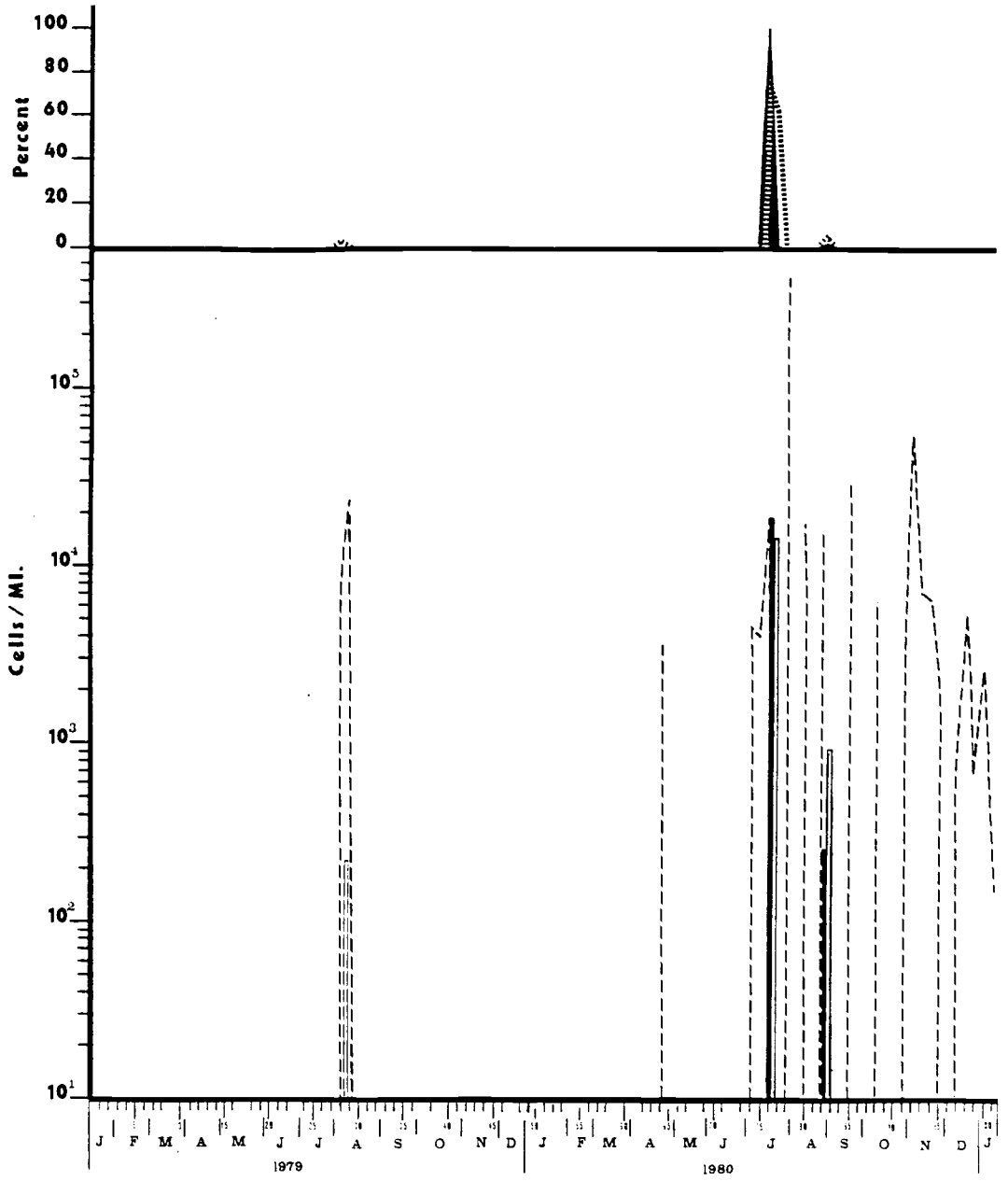


Figure 15. The abundance of Dictyosphaerium ehrenbergianum and its parasite, Aphelidium chlorococcarum. The lower graph shows the number of: host cells/ml each week .▬▬., infected host cells (black bar), and dead host cells (white bar) plotted on a logarithmic scale. In the upper graph are the percentages of infected (solid) and dead (▮▮▮▮▮▮▮▮) host cells. Missing data for parasite abundance is indicated by deletion of the tick mark for that week on the horizontal axis.

Order: Volvocales
Family: Phacotaceae

Pteromonas angulosa

P. angulosa occurred mainly in 1979, sporadically from February through June, and briefly in November. The densest population was observed in June (9200 cells/ml). In 1980, this species was absent except on two dates in the fall.

In 1979, two weeks before the P. angulosa population maximum in June, 23% of the population was infected with zoospores resembling Aphelidium chlorococcarum and 59% of the host cells were dead (Fig. 16). After the population of P. angulosa declined, the fraction of parasitized cells increased to 87%, and 33% of the P. angulosa cells were dead. Dead cells of P. angulosa were present in samples through July, a month after all living cells had disappeared. In the fall, 60% of the P. angulosa population was infected by Aphelidium prior to an increase in the number of host cells. Parasites were absent in 1980 when the host was rare.

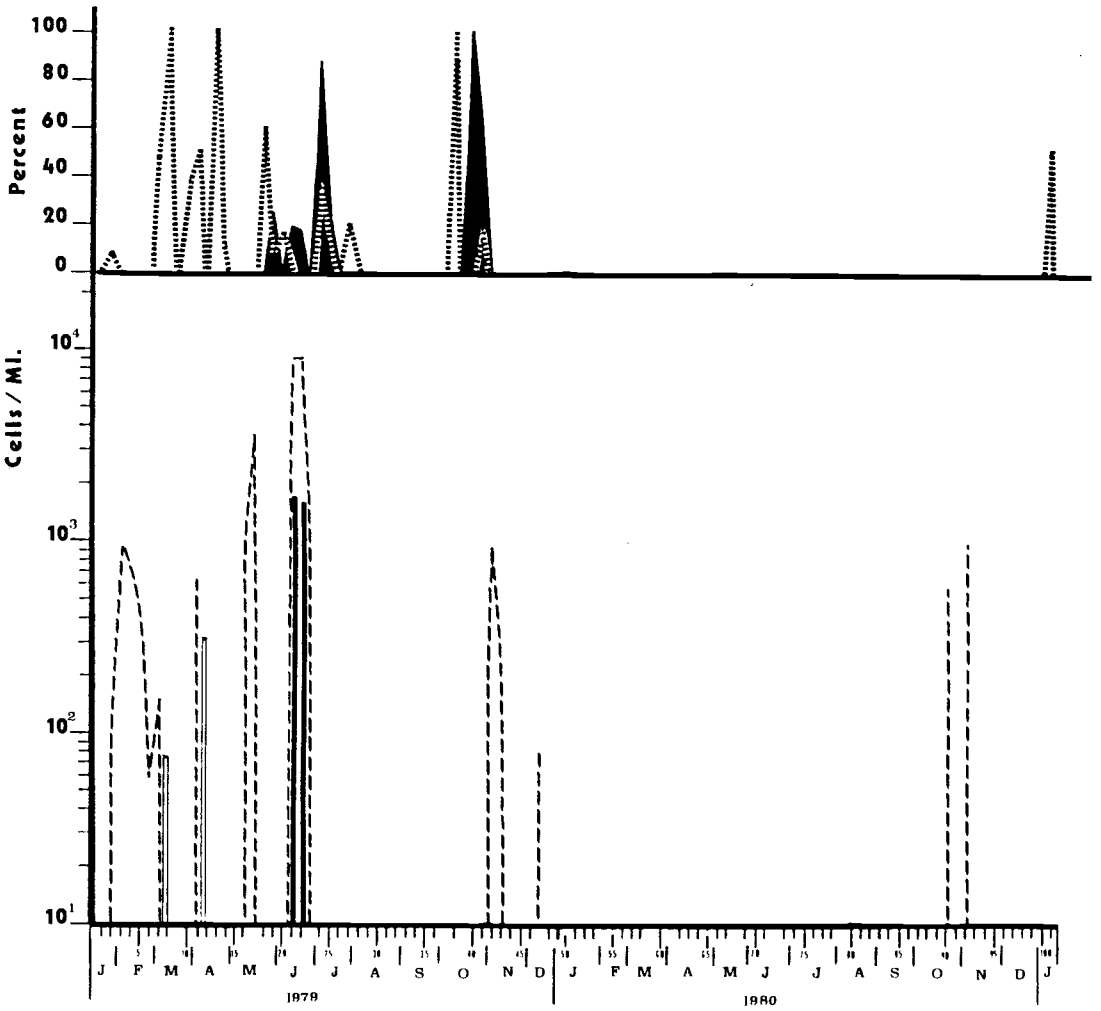


Figure 16. The abundance of Pteromonas angulosa and its parasite, Aphelidium chlorococcarum. The lower graph shows the number of: host cells/ml each week ▬▬▬, infected host cells (black bar), and dead host cells (white bar) plotted on a logarithmic scale. In the upper graph are the percentages of infected (solid) and dead (▮▮▮▮▮▮▮▮) host cells. Missing data for parasite abundance is indicated by deletion of the tick mark for that week on the horizontal axis.

Order: Volvocales
Family: Phacotaceae

Pteromonas sp. 1

Pteromonas sp. 1, a new species similar to P. spinosa Nygaard, was abundant in 1979 from April until August and again in November. In 1980, it was observed mainly in April and May. The maximum numbers occurred in July of 1979 (80,000 cells/ml) and in April of 1980 (59,000 cells/ml).

No zoospores of Aphelidium were observed in 1979, but dead Pteromonas sp. 1 cells were very common from March through August (Fig. 17). High percentages of dead host cells occurred in March (100%) when the host first appeared, in April (100%), in May (66%) during the host increase, and in August (100%) as the host population declined. No parasites were observed on Pteromonas sp. 1 during the fall. In 1980, Aphelidium zoospores were only observed on 6% of the host cells on the date of the Pteromonas sp. 1 April maximum.

Order: Volvocales
Family: Chlamydomonadaceae

Chlamydomonas pertusa

C. pertusa was observed from November to July each year. Parasites were rare. In April and May of 1980,

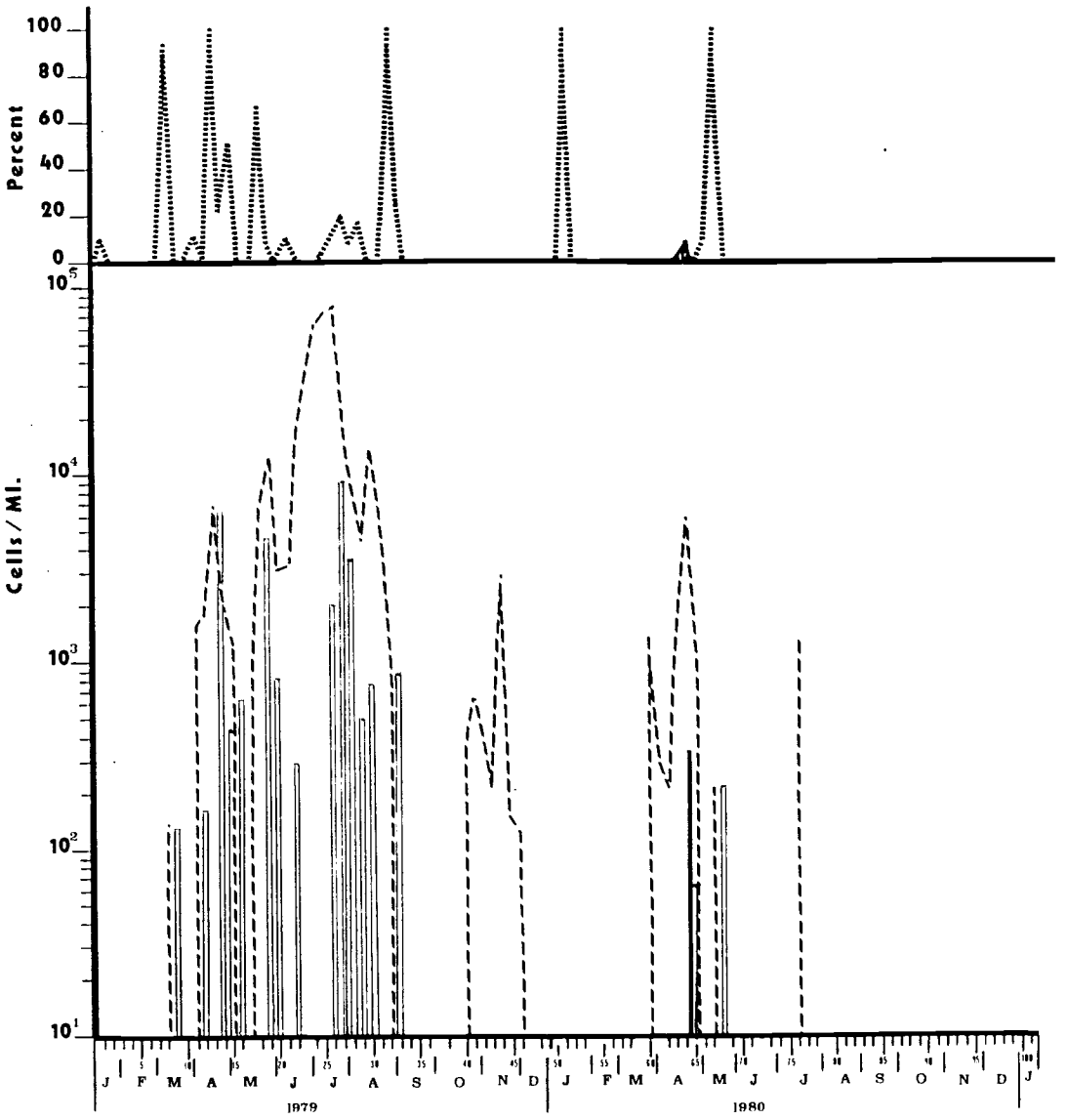


Figure 17. The abundance of Pteromonas sp.1 and its parasite, Aphelidium chlorococcarum. The lower graph shows the number of: host cells/ml each week ▬▬▬, infected host cells (black bar), and dead host cells (white bar) plotted on a logarithmic scale. In the upper graph are the percentages of infected (solid) and dead (▪▪▪▪▪▪▪▪) host cells. Missing data for parasite abundance is indicated by deletion of the tick mark for that week on the horizontal axis.

low levels of an unidentified Rhizophydium species was observed parasitizing C. pertusa in two samples (Fig. 18). No dead C. pertusa cells were observed, and the host population seemed to be relatively unaffected by the Rhizophydium.

Order: Volvocales
Family: Chlamydomonadaceae

Chlamydomonas ovata

Chlamydomonas ovata was abundant from January through August of 1979, and during most of 1980 except for the late summer. No distinct peak populations occurred.

An unidentified Rhizophydium species was the only parasite observed on C. ovata. In 1979, a few infected C. ovata cells were observed in January, April, July and November (Fig. 19). Low frequencies of dead cells were the main indication of parasitism after July. In 1980, Rhizophydium was present periodically throughout the period of C. ovata abundance from February to July. Maximum infections were in March (9%) and in May (16%). There was no evidence of parasitism during the fall.

Summary of Parasite Abundance

Eight of fourteen species of algae suffered the most severe infections (Table 4). All but one of these

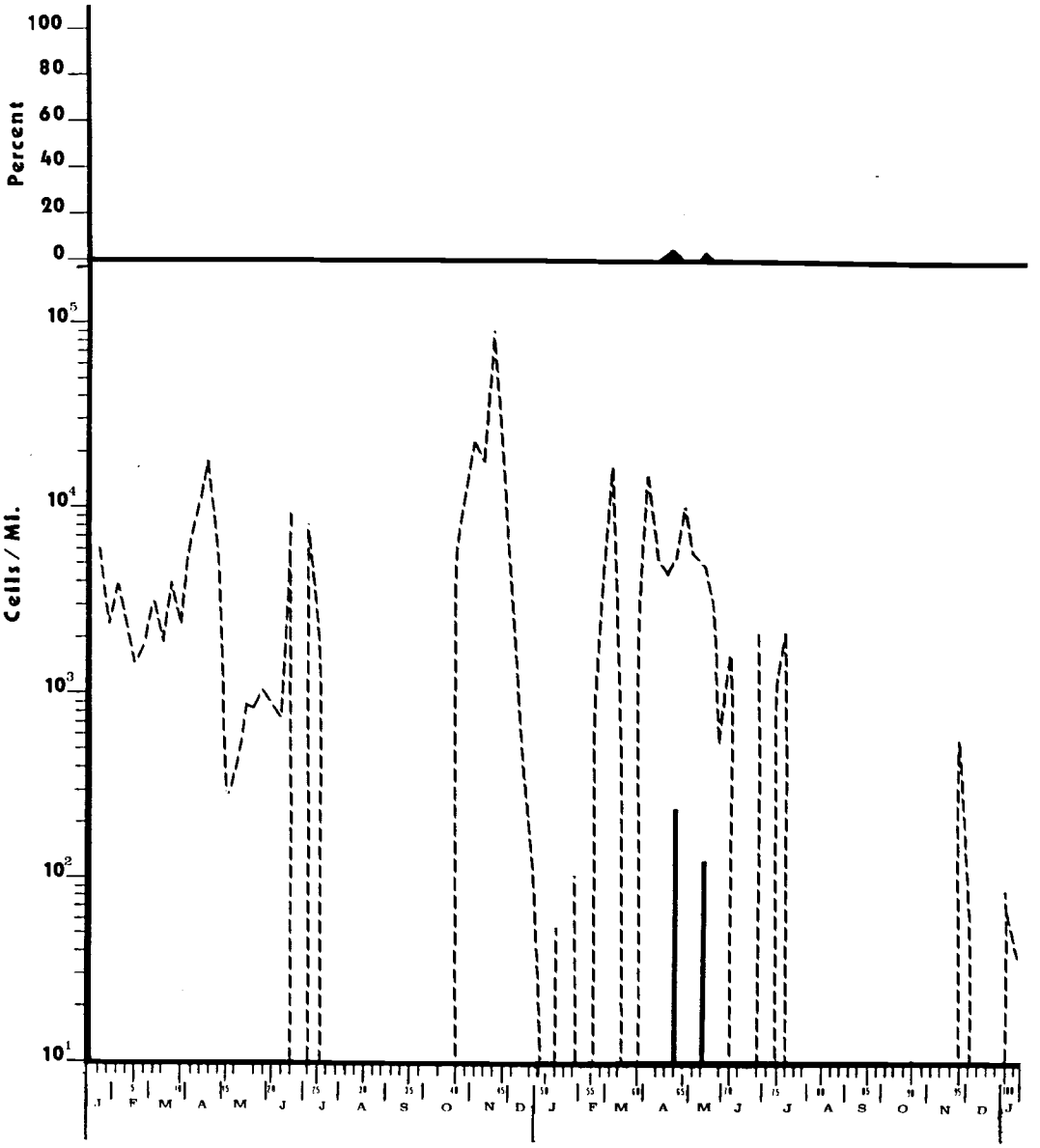


Figure 18. The abundance of Chlamydomonas pertusa and its parasite, Rhizophydium sp. The lower graph shows the number of: host cells/ml each week .—.—.—, infected host cells (black bar), and dead host cells (white bar) plotted on a logarithmic scale. In the upper graph are the percentages of infected (solid) and dead (▪▪▪▪▪▪▪▪) host cells. Missing data for parasite abundance is indicated by deletion of the tick mark for that week on the horizontal axis.

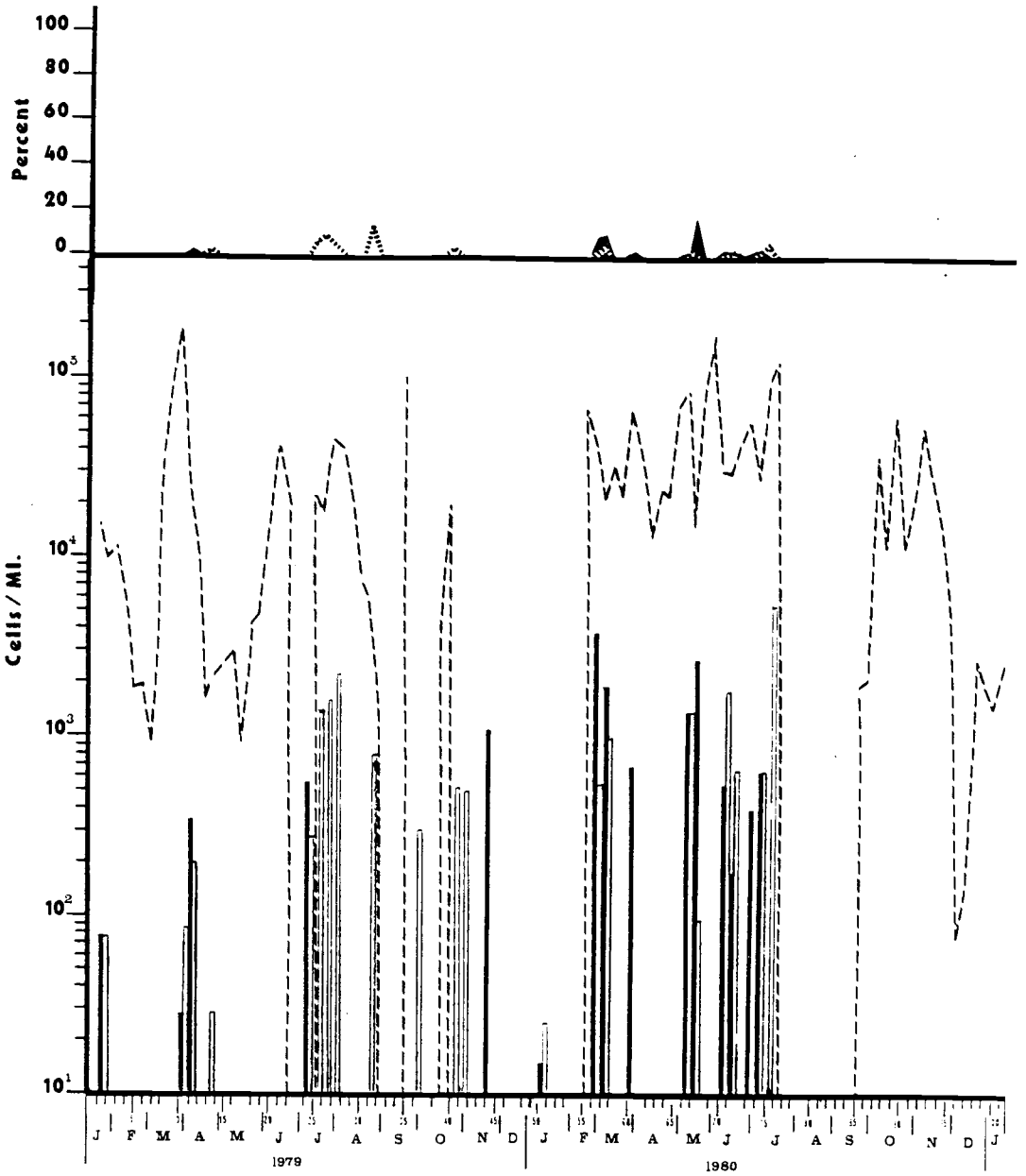


Figure 19. The abundance of Chlamydomonas ovata and its parasite, Rhizophydium sp. The lower graph shows the number of: host cells/ml each week ▬▬▬, infected host cells (black bar), and dead host cells (white bar) plotted on a logarithmic scale. In the upper graph are the percentages of infected (solid) and dead (▪▪▪▪▪▪▪▪) host cells. Missing data for parasite abundance is indicated by deletion of the tick mark for that week on the horizontal axis.

Table 4. Summary of the most significant episodes of parasitism.

Host Species	Parasite	Date	Max % Infection	Max % Dead hosts	Where in Growth Cycle	Effect of Parasites on Host Growth
Scenedesmus obliquus	Aphelidium chlorococcarum and Chytrid Species 1.	Jun '79	26%	20%	Beginning of increase	Brief decline.
"	"	Jul '79	8%	7%	Increasing	None
"	"	Oct '79	9%	9%	Just after maximum	Brief, severe decline
"	"	Dec '79	13%	13%	Declining	Continued declining
"	"	Jun '80	11%	3%	Beginning of increase	Brief, small decline
"	"	Jul '80	25%	19%	One week before maximum	Severe, brief decline
"	"	Aug '80	8%	4%	Declining	Continued rapid decline
Scenedesmus armatus	Aphelidium chlorococcarum	Apr '79	33%	36%	Increasing	Brief decline
"	"	May '79	20%	58%	Increasing	Brief, severe decline
"	"	Jun '79	17%	31%	Maximum	Brief, severe decline
"	"	Jul '79	74%	64%	Increasing	Brief, very severe decline
"	"	Nov '79	17%	40%	Declining	None
"	"	Apr '80	10%	2%	Declining	Brief decline
"	"	Jun '80	22%	10%	Increasing	Brief decline
"	"	Jul '80	56%	23%	Increasing	Brief, severe decline
"	"	Aug '80	54%	37%	Increasing	Brief, severe decline
"	"	Oct '80	42%	30%	Declining - 2 wks after maximum	Severe, continued decline
Scenedesmus acuminatus	"	Jun '80	7%	6%	Increasing	None
"	"	Sep '80	0%	21%	Decreasing	Brief decline
Actinastrum hantzschii	"	Jun '79	0	87%	Maximum	Decreased gradually
"	"	Jul '80	25%	74%	Declining - 1 wk after maximum	Continued, rapid decline
Ankistrodesmus falcatus	"	Mar '80	10%	5%	Maximum	Declined
"	"	Jul '80	100%	37%	Declining - 1 wk after maximum	Declined
"	"	Oct '80	50%	33%	Declining - 3 wks after maximum	Declined rapidly
Tetraëdron minimum	"	Oct '80	46%	35%	Declining - 2 wks after maximum	Declined
Dictyosphaerum ehrenbergianum	"	Jul '80	100%	76%	Fluctuating	Unclear
Pteromonas angulosa	"	Jul '79	87%	33%	Declining	Declined rapidly
"	"	Oct '79	100%	17%	Increasing	Unclear

hosts is in the order Chlorococcales. Aphelidium chlorococcarum was the sole parasite on all of these hosts except that S. obliquus was simultaneously infected by Chytrid Species 1. It is clear from Table 4 that many of the severe epidemics occurred in July, and secondarily in October; when the hosts were most abundant. Scenedesmus obliquus and S. armatus were severely parasitized more frequently than any of the other species. The most severe infections of S. obliquus (26% and 25%) occurred during the summer increase in the population each year in June or July. Although it was subject to more severe parasitism (74% and 56%), severe infections of S. armatus also occurred in July each year when the host population was increasing rapidly. Similarly, the most severe infections occurred on the other six host species in July or October.

Total parasites compared to environment

The combined abundance of all host species subject to parasitism by Aphelidium chlorococcarum and Chytrid Species 1 is compared to the total number of parasite zoospores in Fig. 20 and Appendix C. The curve of host abundance essentially represents the combined counts of Scenedesmus species, because these were considerably more abundant than the other species. Host species

Figure 20. The total number of Aphelidium chlorococcarum and Chytrid Species 1 zoospores relative to the total host abundance and climatic factors each week. The lower graph shows: the total number of infected host cells/ml ▮▮▮▮▮▮▮▮▮, and the number of encysted zoospores/ml of Aphelidium chlorococcarum and Chytrid Species 1 on all of the hosts (black bars) plotted on a logarithmic scale. Each "e" on the bar represents an infection more severe than 10% on one of the hosts. Missing data for parasite abundance is indicated by deletion of the tick mark for that week on the horizontal axis. Climatic data is shown in the upper graphs for each weekly interval between sampling dates. Light intensity is the weekly mean of the total langleys/day. No data was available for September each year. Temperature is the weekly mean minimum soil temperature at a depth of 20 cms which approximates the water temperature. Precipitation is the weekly mean of the total cms per day.

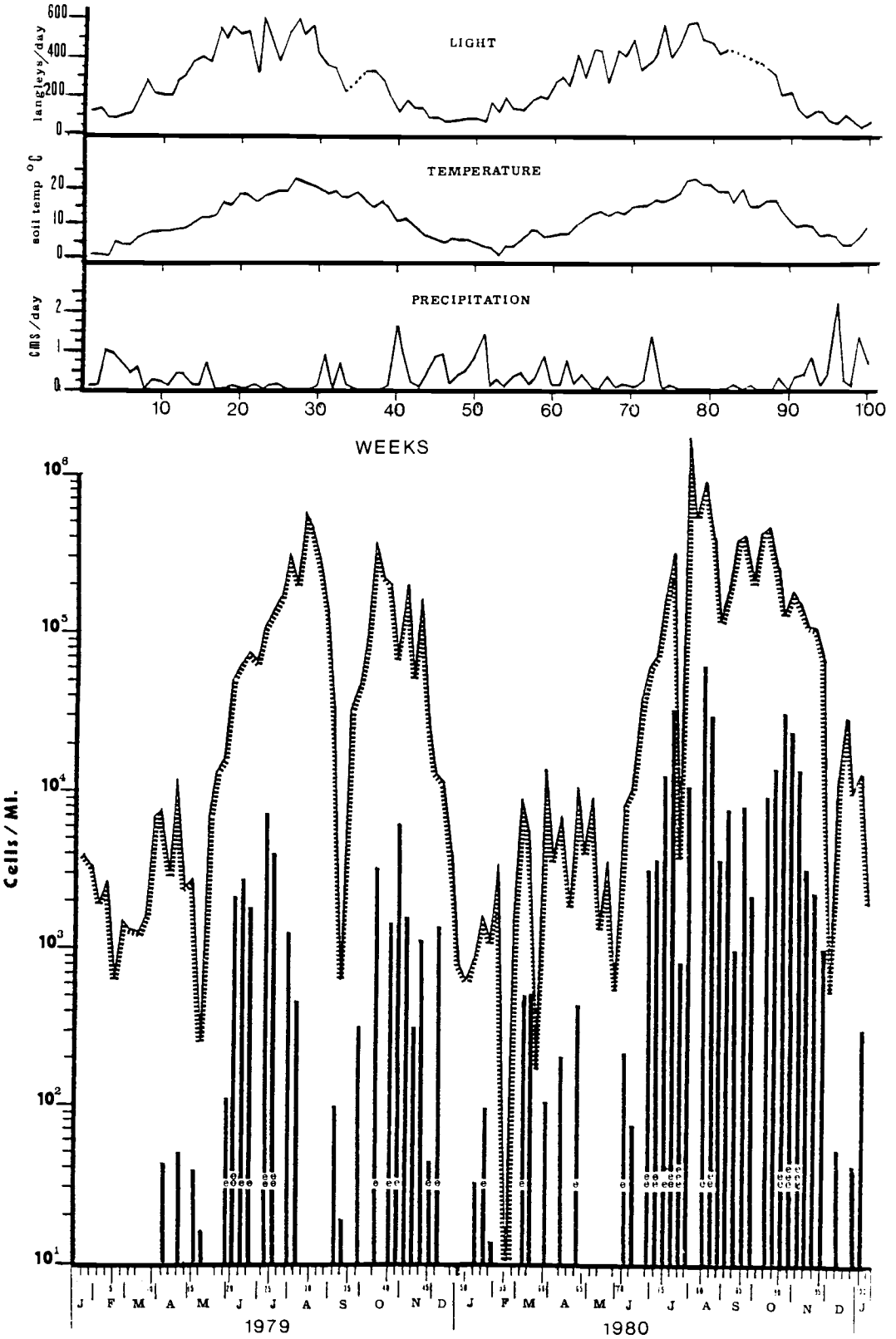


Figure 20. The total number of Aphelidium chlorococcarum and Chytrid Species 1 zoospores relative to the total host abundance and climatic factors each week.

were most abundant from June through November each year, except for a decline in September of 1979. The maximum number of cells of all host species occurred in early August (577,000 cells/ml) and October (374,000 cells/ml) of 1979 and at the end of July (1,818,000 cells/ml) and October (474,000 cells/ml) of 1980. The abundance of host species closely paralleled seasonal changes. The summer maxima coincided with the annual maximum temperature and light intensity and minimum amount of precipitation. The annual decline to sparse populations in December accompanied the onset of winter weather. Furthermore, the decline in September of 1979 was associated with unseasonably high precipitation.

Zoospores of Aphelidium chlorococcarum were observed in most months of the study period and were probably present continuously at low levels. Generally from 1% to 10% of the total host population was infected. Consequently the number of parasite zoospores closely paralleled the abundance of host species. When the host cell density was less than 10^4 cells/ml, low levels of infection (about 1%) were typical. As the number of host cells increased, the number of parasites also increased and the incidence of severe infections was greater. Maximum numbers of zoospores were observed in July (7,000 cells/ml) and October

(6,000 cells/ml) of 1979, and in 1980 in August (64,000 cells/ml) and October (32,000 cells/ml) during periods of maximum host abundance.

The episodes of severe parasitism (greater than 10%) clustered about certain dates in the summer and fall (Fig. 20). In the summer, these occurred for 7 weeks in June and July of 1979 and for 8 weeks in July and August of 1980. In the fall, severe parasitism was observed in October and December of 1979 and at the end of October, 1980. Severe parasitism often occurred during periods of increasing host abundance.

In the summer, episodes of parasitism began as the host population began its annual increase. Simultaneously there was a marked decline in precipitation along with steadily increasing temperature and light intensity. In the fall, the episodes of more severe parasitism occurred with the onset of increased precipitation and while the hosts were abundant.

Description of Parasites

Three parasites of algae were observed in the sewage lagoon near the Corvallis Airport. Two of these, described briefly below, were Chytridiomycetes, Rhizophydium sp. and an unidentified species designated Chytrid Species 1. The third parasite, Aphelidium chlorococcarum, was the most common of the parasites.

It occurred more frequently and infected more species of algae than the other parasites. Aphelidium chlorococcarum was cultured on algal hosts isolated from the lagoon. Its taxonomic status, life history, morphology and ultrastructure were investigated, and the results are reported here.

Chytrid Species 1

Chytrid Species 1 parasitized Scenedesmus obliquus in the sewage lagoon commonly during November of 1979, but it was rare during the remainder of the two year study. Classification of this parasite will require clarification of its life history. It appears to have a single inoperculate sporangium and a holocarpic, endobiotic thallus. These traits suggest tentative placement in the family Olpideaceae, order Chytridiales. However, it is unlike any of the previously described genera in this family.

The encysted zoospore is spherical, 3-4.7 µm in diameter on an infection tube 2-3 µm long X 1-2 µm wide. The infection tube is frequently bent at an angle to the long axis of the host cell. The zoospore characteristically attaches to the apices of the Scenedesmus cells which appear to be indented at the point of attachment.

Several stages of infection were accompanied by increased disorganization of the host cytoplasm. The intracellular parasite was observed just after germination of the cyst (Fig. 21-a&b). The empty cyst wall was persistent on the parasitized host cell. The hyaline intracellular parasite contained fine granules and irregular globules. In another stage, the parasite occupied the encysted zoospore as well as the inside of the host cell (Fig. 21-c&e). Two possible interpretations of this stage are: the cyst has just germinated and the contents are entering the host cell, or the intracellular parasite is re-entering the cyst from the host cell. It may form a sporangium in the cyst. Evidence supporting the second idea is the already very disorganized host cytoplasm and the slightly larger size of the cyst. If, however, the stages observed in Fig. 21-d,f&h are the sporangium, then Fig. 21-c&e more likely represents early germination.

Another stage of the development of the parasite (Fig. 21-d,f&h) may be a developing sporangium or resting spore. This structure was ellipsoidal, approximately 5 µm wide X 9 µm long and was filled with irregular globules in a granular matrix. In one instance (Fig. 21-i), a thick wall, reminiscent of resting spore walls, surrounded the intracellular parasite.

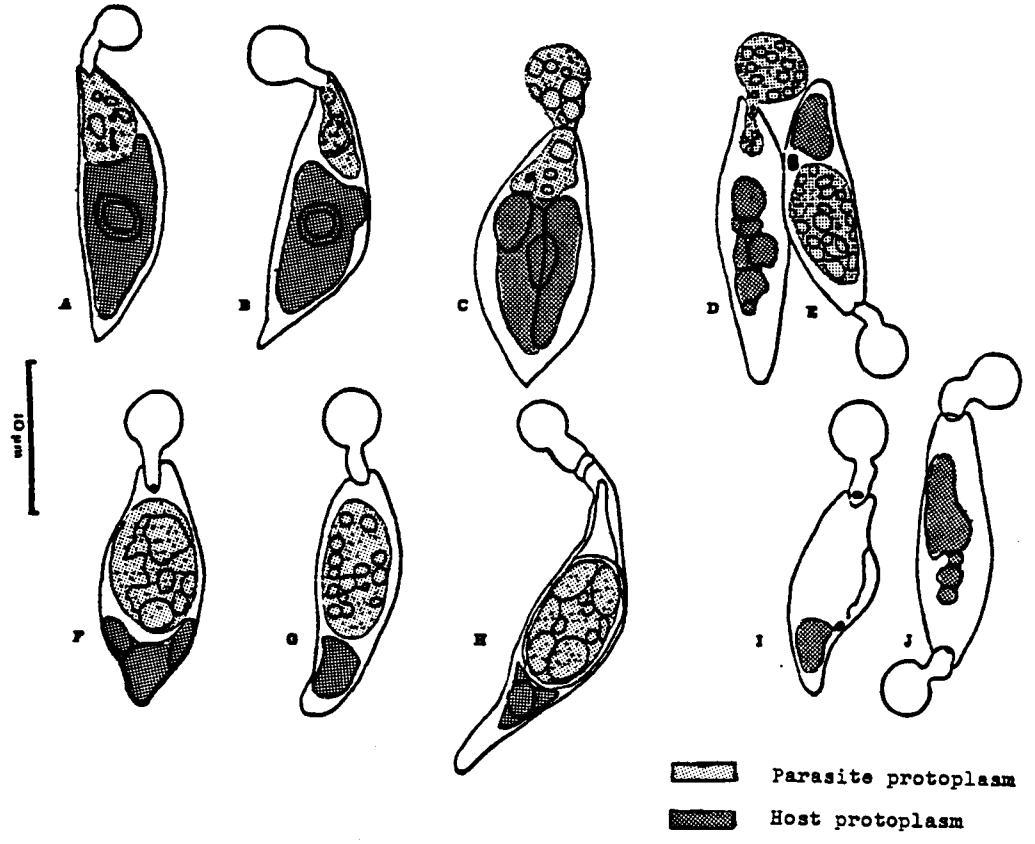


Figure 21. Stages in the infection of Scenedesmus obliquus by Chytrid Species 1.

A&B. Early stage of infection. Encysted zoospore has germinated, and the contents have entered the host cell. The empty wall of the cyst remains attached to the host cell apex.

C&D. Parasite present both intracellularly and in the germinated cyst. Host cytoplasm extensively disrupted by parasitism.

E,F&G. Developing sporangium or resting spores. Note empty cyst wall and remains of host cytoplasm.

H. The thick wall around the intracellular parasite resembles a resting spore.

I&J. Empty walls of parasitized host cells with empty cysts attached. Remnants of host cytoplasm are visible. Apparently zoospore discharge has occurred but no exit pore is visible. Fig. 21-I. Zoospores may have been discharged by rupture of the right side of the host cell. Fig. 21-J. Two parasite zoospores infected this host cell.

After zoospore discharge, the parasitized host cells with the cyst wall still attached were empty except for the green remnants of the host cytoplasm at the end opposite the cyst (Fig. 21-i&j). The mechanism of zoospore discharge was unclear; no exit tube through the host or cyst walls was apparent. Release of the zoospores may be achieved by rupture of the host cell wall (Fig. 21-i).

Rhizophydium sp.

Zoospores of Rhizophydium sp. encyst on the posterior apex of a Chlamydomonas ovata cell (Pl. VII-1&2). Encysted zoospores, 2 µm in diameter, contain one or several globules. A single, thickened axis arises from the sessile cyst and penetrates the host wall. Inside the cytoplasm of the host cell a much branched rhizoidal system originates from this axis (Pl. VII-5). The encysted zoospore enlarges into the sporangium. The sporangium is globose or slightly flattened, 3 to 8 µm high X 3 to 6 µm broad, and contains many irregularly sized globules (Pl. VII-3,4&5). Zoospores in the mature sporangium contain at least one oil globule (Pl. VII-6). Dehiscence of the sporangium, motile zoospores and resting spores were not observed.

Aphelidium chlorococcarum Fott

Following is a description of the life history, structure, and ultrastructure of a strain of Aphelidium chlorococcarum grown in laboratory culture on several host species. These included three species isolated from the Corvallis Airport sewage lagoon: S. acuminatus (Lag.) Chodat., S. armatus (Chod.) Smith and S. obliquus (Turp.) Kutzing. One other species -- S. obliquus (Pring.) UT72 -- was from the University of Texas Culture Collection.

Briefly, the life history of Aphelidium chlorococcarum is as follows. A zoospore attaches to a potential host cell. The zoospore sheds the flagellum, encysts and forms a short germ tube (Pl. I-1&2). The encysted zoospore is the only phase of the life cycle where Aphelidium chlorococcarum has a cell wall. The contents of the encysted zoospore enter the host cell through the germ tube. The intracellular parasite consumes the host cytoplasm and eventually fills the entire space within the host cell. The intracellular parasite is hyaline and contains an orange globule that is presumably the undigested remains of the host cytoplasm (Pl. I-8&9). The only wall around the parasite at this stage is the cell wall of the dead host. Numerous lipid globules appear in the intracellular

parasite (Pl. I-8). Cytoplasmic cleavage of the parasite results in formation of the sporangium and approximately 16 zoospores. The number of zoospores depends on the size of the host cell. The zoospores exit from the dead host cell, probably through the germ tube pore after the old cyst wall breaks off. The liberated zoospores infect new host cells and the cycle begins again.

The morphology of A. chlorococcarum was observed with Differential Interference Contrast (D.I.C.) microscopy and a transmission electron microscope (T.E.M.). The stages observed were the zoospores, encysted zoospores, germination of the cyst, development of the intracellular parasite into a sporangium, the empty sporangium, and one possible resting spore.

Zoospores of A. chlorococcarum are spherical or pointed ellipses, 2 µm in diameter; with a single, 9 µm long, posterior whiplash flagellum (Fig. 22 - A&G). Inside of the zoospores, four lipid globules and a large, ring-shaped nucleus, 0.8 µm in diameter, are visible with D.I.C. No electron micrographs of motile zoospores were obtained, although zoospores were abundant in the cultures. They appear to have been destroyed by the fixation process.

Nonmotile zoospores were observed with D.I.C. (Fig. 22 - C to F). The retracted flagellum was some-

Figure 22. Aphelidium chlorococcarum observations. H-Q are to the scale shown. A-F. Zoospores observed with phase contrast at 1350x.

A. Typical zoospore with 4 lipid globules and nucleus visible.
B. Zoospore with 2 sets of organelles.
C. Nonmotile zoospore with retracted flagellum.
D. Differently sized, attached zoospores with retracted flagella, possibly gametes.
E. Nonmotile zoospore with double organelles.
F. Nonmotile zoospore with flagellum recently retracted.
G. Typical zoospore viewed with the light microscope with 3 of the lipid globules, the nucleus, and whiplash flagellum visible.
H. Encysted zoospore on uninfected Scenedesmus acuminatus.
I. S. acuminatus coenobium with cysts and 2 developing A. chlorococcarum intracellular parasites.

J-L. Sporangium development in Scenedesmus obliquus.
J. Immature sporangium.
K. Mature sporangium with lipid globules visible in zoospores, and exit tube.
L. Discharged sporangium with waste globule, exit tube, and ungerminated zoospore cyst.
M. Resting spore in S. acuminatus.

N-Q. Infection of an S. obliquus cell during a 30 hour period.
N. Initial observation during early development.
O. 18 hours. Host cell half digested. Orange waste globule now present within the parasite vacuole.
P. 26 hours from initial observation. Host wall filled with the parasite.
Q. 30 hours. Lipid droplets appearing in the immature sporangium.

R-T. Reconstructed drawings of electron micrograph serial sections of A. chlorococcarum.
R. Ungerminated cyst on empty S. armatus cell wall with nucleus, 3 lipid globules, microbody? and unidentified vesicle (Pl. III-1).
S. Ungerminated cyst on live S. obliquus UT72 cell showing nucleus, 3 lipid globules and distal vacuole (Pl. III-3).
T. Transverse section of infected S. obliquus UT72 cell wall containing maturing zoospores of A. chlorococcarum (Pl. VI-1 to 3).

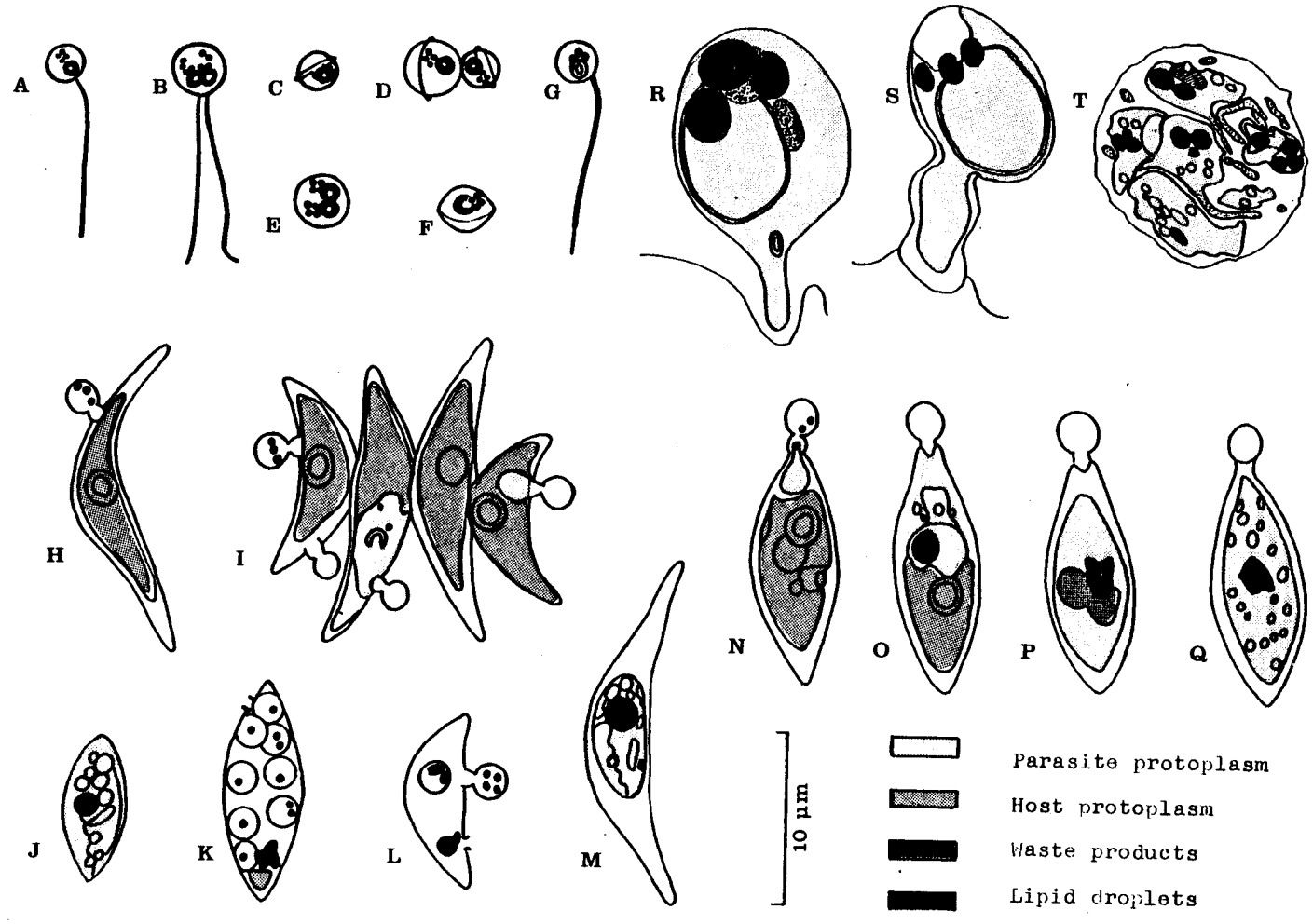


Figure 22. Aphelidium chlorococcarum observations.

times visible wrapped around the circumference of the cell. Flagellar retraction was observed on one occasion with D.I.C. at 1250X magnification. A zoospore was floating in a sealed water mount with the flagellum extended but motionless. Suddenly the cell changed from a sphere to a pointed ellipse with a rapid jerk, and the flagellum disappeared. A careful search of the surrounding medium failed to reveal a detached flagellum. The flagellum appeared to be wrapped around and inserted at the apices of the elliptical cell (Fig. 22-F). In the next 15 minutes, the cell gradually became more rounded but did not extend the flagellum again. Held (1973) obtained T.E.M. sections of a similarly wrapped flagellum in Rozella, an endobiotic chytrid.

Occasionally zoospores had two flagella (Fig. 22-B). Also, larger zoospores, 4 µm in diameter, with eight lipid globules in two clusters and with two nucleii were observed with or without flagella (Fig. 22 - B&E). These suggest either syngamy or incomplete cleavage. Once two unequally sized adherent zoospores were observed (Fig. 22-D) that could be gametes fusing. Otherwise, sexuality was not observed.

Encysted zoospores of Aphelidium chlorococcarum, 2 µm in diameter, are attached to the lateral walls of the host by a 1.0 X 0.5 µm germ tube. Electron micro-

graphs of the germ tube indicate that it does not penetrate the interior of the host cell wall (Pl. II-4&5 and Pl. III-5&6). Organelles of encysted zoospores visible with D.I.C. are the nucleus and four tightly clustered lipid globules. All four of the lipid globules are generally not visible at the same time in the photographs because they are in different focal planes. The ultrastructure of the encysted zoospore includes a large nucleus surrounded by uniformly dispersed ribosomes (Pl. II-1 and III-1&3). Also observed was a dense body adjacent to the nucleus that may be a mitochondrion or microbody (Pl. III-1&2). Both mitochondria and organelles resembling microbodies, as defined by Vigil (1973), are visible in a germinated cyst (Pl. II-2). Serial sections reveal lipid globules clustered about a distal vacuole (Pl. III-3 and Fig. 22-S).

After germination of an encysted zoospore occurs, the contents of the cyst move through the germ tube into the host cell. Lipid globules are visible with the light microscope at first in the cyst and then in the germ tube (Pl. I-5). The empty wall of the cyst remains attached to the host cell as the intracellular parasite grows (Pl. I-7). Electron micrographs also show the contents of the germinated cyst moving through the germ tube from the cyst wall into the host cell

(Pl. II-4,5&6 and Pl. III-4). As germination occurs, the distal vacuole increases in size (Pl. II-2,4,5&6 and Pl. III-2,4,5&6) until remnants of cytoplasm are all that remain in the cyst wall (Pl. II-6).

Germination of the cyst is followed by the gradual enlargement of the intracellular parasite (Fig. 22-N to P). When observed with D.I.C., the parasite is hyaline and finely granular. After approximately half of the host cytoplasm has been consumed, a characteristic orange waste globule appears in a vacuole in the parasite (Fig. 22-0 and Pl. I-8). Growth continues until the host cytoplasm is consumed completely and the parasite fills the interior of the host cell wall. The ultrastructure of the intracellular parasite includes mitochondria, lipid globules, a large vacuole, and membrane-bound organelles that may be microbodies or multivesicular bodies (Pl. II-3 to 6 and Pl. III-4). These are found in a matrix of uniformly distributed ribosomes and fragments of endoplasmic reticulum.

Formation of the sporangium and zoospores from the intracellular parasite occurs by cytokinesis. The developmental phase prior to cleavage is the immature sporangium. Observed with D.I.C., the immature sporangium is characterized by lipid globules in a hyaline matrix and a vacuole containing the orange waste

globule (Pl. I-8 and Fig. 22-Q). After cytokinesis, the mature sporangium is filled with tightly packed zoospores, each containing a cluster of four lipid globules (Pl. I-9 and Fig. 22-K). I counted 22 zoospores in the sporangium shown in Pl. I-9. The zoospores are amoeboid in shape and flagella are visible in the mature sporangium (Pls. IV, V-1 and VI-1 to 5). The ultrastructure of zoospores in the sporangium (Pl. IV and V-1) is similar to that of the encysted zoospores. A large nucleus is closely associated with a cluster of lipid globules and a mitochondrion. A possible microbody and fragments of endoplasmic reticulum are the only other visible structures. Also visible is a vacuole containing many electron dense particles, presumably the undigested remains of the host cytoplasm (Pl. V-1). No wall other than the cell wall of the host surrounds the zoospores in the zoosporangium.

Emergence of the zoospores from the sporangium was not observed. However, there was evidence that the zoospores escape through the germ tube after the empty cyst wall breaks off. On one occasion, a cluster of eight quiescent zoospores was observed outside of a host wall with their flagella all oriented toward an 0.5 µm long by 0.5 µm diameter exit tube (Pl. I-4 and Fig. 21-K&L). This was the only opening observed on any of the parasitized host cells. As it is the same

size as the germ tube, and empty cysts were generally not observed on cells where an exit tube was present, it seems probable that the germ tube becomes the exit tube when the cyst wall breaks off. Similarly, Scherffel (1925) hypothesized that the zoospores of Aphelidium tribonemae escaped through the germ tube pore.

Recently emptied sporangia contain a residual material (Pl. V-2). I have often observed bacteria inside of recently discharged sporangia that seem to be decomposing this material. After several weeks, empty sporangia no longer contain any residue or bacteria and only the orange globule is visible (Pl. V-3). The orange globules are apparently resistant to degradation as they have been observed in cultures for at least a month after infection by A. chlorococcarum has ceased.

Only a single resting spore was observed in a lagoon sample enriched with Scenedesmus acuminatus. Because A. chlorococcarum was the only parasite observed on S. acuminatus in this culture, it is possible that this is a resting spore of A. chlorococcarum. A composite was drawn of photographs of the resting spore taken at three focal planes (Fig. 22-M). The resting spore had a smooth wall and dense, globular contents. An orange globule was present, but it was

impossible to determine whether it was located inside or outside of the resting spore wall.

Only one of many attempts to determine the generation time of Aphelidium chlorococcarum was successful. The organism studied was a rarely observed form of A. chlorococcarum. It was the same as the typical form except that the cyst was attached apically. Schnepf (1972) also reported apical attachment. The infection process was observed at 1250 X magnification for 30 hours in a lagoon sample sealed under a cover-glass with silicone dessicator sealant. Drawings were traced from photographs of each stage of the infection (Fig. 22-N to Q). In the earliest stage, two of the lipid globules still remained in the cyst. After 18 hours, the host cell was half occupied by the parasite, and contained an orange waste globule. At 26 hours, the host cell was consumed by the parasite and by 30 hours, clusters of lipid globules indicated the formation of an immature sporangium. No further development occurred during the next two days. Apparently the parasite died. These preliminary results indicate that the generation time may be as long as two days, at least under these conditions.

Discussion of *Aphelidium*

The taxonomic basis for the separation of species of *Aphelidium* has received relatively little attention. In the past, species of *Aphelidium* have been distinguished primarily on the basis of the species of host parasitized, and the few morphological traits of *Aphelidium* that are visible with the light microscope (Table 5). Many of these traits may be variable within a strain and therefore not useful taxonomic criteria. Consequently, the differences indicated in the table may be more a reflection of the incomplete state of our knowledge than real differences between the species.

The strains of *Aphelidium* in the sewage lagoon most closely resemble *Aphelidium chlorococcarum* Fott, in the zoospore size, absence of stiletto and in the host species parasitized. They appear to differ from Fotts (1957) description in the zoospore shape, number of lipid globules and the occurrence of phagocytosis, but more study of these traits is needed. Fott (1957) and Schnepf et al. (1971) showed the zoospore with a posterior point, while I only observed spherical zoospores or pointed ellipses. Shape is known to vary, however, so this may not be significant (Koch, 1968; Gromov, 1972b). Fott saw only one lipid globule in the zoospores. The lagoon strain sometimes appeared to

Table 5. Comparative light microscopic traits of *Aphelidium* species.
(- no information available)

Species (author of description)	Host Species Parasitized	Traits						
A. deformans(Zopf)	*Coleochaetae soluta* *C. irregularis*	2-3	S	-	-	-	-	+
A. melosirae(Scherffel)	*Melosira varians*	4	S/O/A	1-4	10	+	-	0
A. cnaetophorae(Scherffel)	*Chaetophora elegans*	2.7	S/O	S	9	-	-	+
A. tribonemae(Scherffel)	*Tribonema sp.*	2-4	S/O/A	S	-	-	-	0
" (Gromov, 1972)	*Tribonema gayanum* *Chloridella neglecta* *Botriodopsis intercedens*	2-3	S/O/A	-	12	+	0	0
A. chlorococcarum (Fott)	*Scenedesmus spps.* *Actinastrum spps.* *Oocystis spps.* *Tetraedron spps.* other Chlorococcales	1.5	O	1	8	-	0	0
" (Schnepf)	*Scenedesmus armatus*	-	O	1/S	-	+	0	0
" (Woods)	*Scenedesmus spps.* (and see Table 3)	2	S	4	9	0(?)	0	0
A. chlorococcarum f. majus (Gromov, 1970a)	*Kirchneriella spps.* *Ankistrodesmus spps.*	2-3	S	1	12-15	+	+	0
" (Gromov, 1975)	*Kirchneriella obesa*	2-3	S	S	11	+	+	0

zoospore size (µm)

zoospore shape: S = spherical
O = ovoid
A = amoeboid

number of lipid globules:
s = several

flagellum length (µm):

phagocytosis: + present/0 absent

stiletto: + present/0 absent

host wall deformed: + yes/ 0 no

have only one lipid globule in the zoospores when viewed with the light microscope, but four distinct globules were resolved in all of the zoospores observed with D.I.C. Further study is needed to determine the variability of the number of lipid globules within a species.

The lagoon parasite was classified as Aphelidium rather than any of the other species of Aphelidium for several reasons. 1) Different species of hosts were infected. 2) Zopf's (1885) incomplete description of A. deformans, a parasite of Coleochaetae, indicated that it caused deformation of the host cell wall, unlike the lagoon strains of Aphelidium. 3) Scherffel's (1925) three species resemble the lagoon strains in: the mode of parasitism, the retention of the empty cyst on the parasitized host, the presence of orange globules in the intracellular thallus, and in several lipid globules in the zoospores. But, Scherffel's species were rejected because A. chaetophorae caused deformation of the host wall, A. melosirae and A. tribonemae had larger zoospores and the zoosporangium of A. melosirae did not fully occupy the interior of the host cell.

Aphelidium chlorococcarum is the only species whose ultrastructure has been investigated (Schnepf et al., 1971; Gromov et al. 1970, 1975). Schnepf et al.

(1971) described the ultrastructure of a strain of Aphelidium that parasitized Scenedesmus armatus in large-scale, outdoor cultures. The ultrastructure of this strain appears different from the lagoon strain in several ways (Table 6). Schnepf et al. found only one large lipid globule in the encysted zoospore, but several globules in zoospores still in the sporangium. I found four lipid globules in the zoospores in both of these stages of development. Schnepf et al. described the germ tube wall as penetrating about 0.5 µm into the host cell lumen and widening into a funnel-like shape. He sometimes found a "plug" of electron-dense material in the tube. The germ tube walls I observed typically did not penetrate beyond the inner edge of the host wall, were cylindrical in shape and did not appear plugged. Schnepf et al. also described more organelles in the encysted zoospore than I observed, but I found mainly cysts at later stages of germination so the organelles may have already entered the host cell. There were no conclusive differences between our observations of the intracellular thallus. Schnepf et al. also claim to have found phagocytotic vacuoles. I found vacuoles, but no evidence whether they were phagocytotic in origin.

Gromov et al. (1970, 1975) isolated Aphelidium chlorococcarum f. majus from large scale outdoor cultures of Kirchneriella obesa. In host range studies, it also infected an Ankistrodesmus sp. but none of 76 strains of Scenedesmus. The zoospores of this strain were unique in the presence of one to several stilettos on the anterior of the cell. They hypothesized these were for attachment to the host cell. Another possibility is that they are pseudopodia.

Gromov (1975) is the only researcher to observe the ultrastructure of motile zoospores of Aphelidium. They contain: a massive nucleus with the chromatin concentrated near the periphery, several anterior lipid globules associated with a large mitochondrion, endoplasmic reticulum and several small organelles that may be microbodies. A kinetosome, dictyosome, and centriole were also observed. The ultrastructure of the encysted zoospore (Gromov and Mamkaeva, 1975) is similar to that observed by Schnepf et al. (1971) and me. Visible are the large nucleus, a mitochondrion and the same dense body (mitochondrion? microbody?) observed by Schnepf. Gromov observed that the germ tube wall of the encysted zoospores terminated at the host wall and there was no plug in the tube, unlike Schnepf's observations.

In summary, this study confirms and elaborates on the work of Fott, Schnepf et al. and Gromov et al. on the structure and life history of A. chlorococcarum. Electron micrographs of the parasite on three Scenedesmus species as well as serial sections provide additional ultrastructural data. Evidence is cited that zoospores exit from the zoosporangium through the germ tube pore as Scherffel (1925) mentioned for A. tribonema. Other new contributions include the observation of biflagellate zoospores with 2 nuclei and 2 lipid globule clusters, partially fused zoospores which may be gametes, and zoospores with the flagellum retracted. the cell wall. Retraction of the flagellum was observed Part of the infection process was documented for 36 hours from the time of host penetration to formation of an immature sporangium.

Taxonomic status of the genus Aphelidium

Aphelidium has been classified as a parasitic protozoan in the class Flagellatae, Order Mondinae, and family Gymnococcaceae ever since the genus was established by Zopf (1885). However, some authors have observed that Aphelidium bears a striking resemblance to some Chytridiomycete fungi, in particular, members of the Olpidiaceae (Held, 1973). Gromov and Mamkaeva

(1975) and others have suggested that the similarity might be explained by convergent evolution and by adaptation to parasitism.

It seems that Aphelidium was originally considered a protozoan due to the absence of a parasite cell wall around the endobiotic thallus. This criterion is problematical since Held (1980) has shown that Rozella allomyces (a chytrid fungus) also lacks an endobiotic cell wall. Both genera have walls at other stages of the life cycle; around the encysted zoospores, and the resting spores. Later, Scherffel (1925) distinguished monads from chytrids according to multiple or single lipid globules, respectively. Since some chytrids have multiple lipid globules and reports vary on the number of lipid globules in Aphelidium, this criterion must be rejected.

If Aphelidium is diagnosed according to Sparrow's (1960) key, it fits all criteria for the Olpidiaceae. Aphelidium is holocarpic (lacks specialized vegetative structures), monocentric, and forms one inoperculate sporangium from each initial cell. The zoospore is posteriorly uniflagellate. The genus within this family that most closely resembles Aphelidium is Rozella, especially in the absence of a walled endobiotic thallus (a trait atypical of other chytrid genera) and in the absence of a specialized sporangial

discharge apparatus. Cornu's criteria for Rozella were listed by Sparrow (1938).

1. Parasitic on other aquatic fungi.
2. Sporangium wall "fused with the host wall".
3. Zoospores escape from a pore formed by papilla dissolution.
4. Plasmodial thallus.
5. Spherical resting spores within spiny walls and no companion cells.
6. Infected host cell may swell.

Of these, Sparrow's key (1960) emphasizes the "fusion of the parasite and host walls" which has since been shown by Held (1980) to be no parasite wall at all. Aphelidium and Rozella both lack an endobiotic wall, have a plasmodial thallus, and may cause swelling of the host wall. Since the discharge of Aphelidium zoospores has not yet been observed, it is not known whether Aphelidium has a discharge papilla like Rozella. Aphelidium is not only similar to Rozella in morphology and in the infection process, but also the zoospores move similarly.

The differences, according to Cornu's critieria, are the presence of spiny or smooth walled resting spores and whether the host is algal or fungal. Spiny walls are not characteristic of all Rozella species, R.

parva has a crinkled wall but no spines (Canter, 1969). Rozella has been found only on fungal hosts, while Aphelidium is known only on algal hosts. Aphelidium and Rozella could also be distinguished by whether orange-brown degradation products occur, but this may simply reflect that only the algae have carotenoids that are indigestible by these parasites. Cross inoculation experiments, such as attempting infection of fungi with Aphelidium and algae with Rozella would be informative.

Ultrastructural studies on both genera have revealed other differences that may justify keeping the genera separate. Lange and Olson (1979) considered zoospore ultrastructure the most conservative, valid taxonomic character at present. They compiled a table of ultrastructural traits of zoospores of diverse uniflagellate Phycomycetes. Part of their table is repeated in Table 6 to compare the data available on A. chlorococcarum with data on Olpidium and Rozella. Of the three criteria considered most important in chytrid taxonomy by Lange and Olson (ribosome arrangement; number, size and shape of mitochondria; and structure of the microbody-lipid complex) only ribosome arrangement is the same in all three genera. The limited data on Aphelidium zoospores (Gromov and Mamkaeva, 1975) suggests there is only one large mitochondrion that is

Table 6. Ultrastructure of Aphelidium, Rozella and Olpidium

	Traits from Lange & Olson							Other traits			
	A. zoospore size class	B. location of nucleus	C. ribosome arrangement	D. mitochondrial organization	E. microbody-lipid complex type	F. endoplasmic reticulum	G. dictyosomes	H. microbody present	I. number of lipid globules	J. encysted zoospore germ tube penetration	K. germ tube plug
Olpidium brassicae zoospore	s	a	1	1	1A	1	0	+	V	n.a.	n.a.
O. pendulum zoospore	m	p	1	3-4	1A	1	1	+	(1)V	+	-
O. radicale zoospore	l	a	1	1	1A	6	1	+	V	-	-
Rozella allomyces zoospore	s	a	1	5c	1A	2	1	+	V(1-7)	n.a.	n.a.
cyst	s	p	1	5c		2	0	+	V	0	0
Aphelidium chloroccarum f. majus zoospore - G	s	c	1	5d	?A	2	1	0	V(2)	n.a.	n.a.
A. chlorococcarum zoospores in zoosporangium - S	s	-	1	5	n.a.	1	1	-	V	n.a.	n.a.
- W	s	c	1	1	n.a.	1	0	+?	4	n.a.	n.a.
encysted zoospores -S	s	c	1	1		1/2	0/1	+	1	+	+
-G	s	c	1	5	n.a.	-	rare	+?	-(0)	0	0
-W	s	c	1	1?		0	0	+?	4	0	0
endobiotic thallus -S	n.a.	n.a.	1	1	n.a.	2	1	0	V(8)	n.a.	n.a.
-G	n.a.	n.a.	1	5	n.a.	-	-	-	-	n.a.	n.a.
-W	n.a.	n.a.	1	1/5	n.a.	2	0	0	V(3-8)	n.a.	n.a.

Table 6. Ultrastructure of Aphelidium, Rozella and Olpidium.

Explanation of notations:

n.a. not applicable
- no information available
0 structure is absent
? not certain until further study
/ either condition exists
-S Schnepf (1971)
-G Gromov (1975)
-W Woods

A. Zoospore size class (spore diameter)
s: 1.5-3 µm
m: 3-5.5 µm
l: 5.5-13 µm

B. Location of the nucleus
a: anterior
c: central
p: posterior

C. Ribosome arrangement
1. The ribosomes are evenly dispersed in the zoospore
2. The ribosomes are loosely aggregated, without a bounding membrane and not delimited by organelles.
3. The ribosomes are aggregated in a nuclear cap area, partially delimited by membranes and/or by organelles.
4. The ribosomes are aggregated in a nuclear cap, completely delimited by a nuclear cap envelope.

D. Organization of the mitochondria
1. Several mitochondria (or few but highly branched mitochondria), without any specialized spatial organization.
2. Several mitochondria, at the periphery of the nuclear cap (area).
3. Several mitochondria, confined to the posterior portion of the zoospore.
4. All mitochondria arranged in a petal-like configuration.
5. A single mitochondrion:
   a. around posterior of nucleus and nuclear cap

b. more around lateral part of nuclear cap
c. spherical between rhizoplast and nucleus
d. posterior between nucleus and side body complex

E. The microbody-lipid body complex
Subgrouping, according to Powell (1978) into types: $1A_1$, $1A_2$, $1A_3$, $1B_2$, 1B, 2, 3, 4A, and 4B.

F. Endoplasmic reticulum
1. Endoplasmic reticulum sparse, a single formation.
2. Multiple configurations of encoplasmic reticulum.
3. An extensive sheet of endoplasmic reticulum.
4. Sheets of endoplasmic reticulum traverse the ribosome containing area.
5. Endoplasmic reticulum partially delimits the nuclear cap area.
6. Rough endoplasmic reticulum encircles the lipid bodies.
7. Endoplasmic reticulum delimits the nuclear cap.

G. Dictyosome
0: No dictyosome observed.
(0): Vestiges of a dictyosome observed.
1: A single dictyosome present.
2: More than one dictyosome present.

H. Microbody
+ present
0 absent

I. Lipid globule number
V variable (the numbers observed)

J. Germ tube penetration
+ tube wall is within host cell lumen
0 tube wall stops at inner layer of host wall

K. Plug in germ tube
+ present
0 absent

closely associated with the microbody-lipid (MBL) complex similarly to the arrangement in Rozella. The position of the mitochondrion in Rozella is immediately posterior to the nucleus, while in Aphelidium it is on the side of the nucleus opposite the MBL complex. Powell's (1978) MBL complex type $1A_3$ has a tight cluster of lipid globules enclosed by a folded ER cisterna on the exterior and a bowl-shaped microbody on the inside. Rozella was the only representative of this type in Lange and Olson's table. Aphelidium's MBL complex most closely resembles type $1A_3$ in that it has tightly clustered lipid globules closely associated with a mitochondrion as well as cisternae on the outside of the cluster. Two unidentified structures in the lipid cluster in Gromov and Mamkaeva's (1975) Fig. 1.2 may be microbodies. Furthermore, the position of the dictyosome in Rozella and Aphelidium is similar.

Gromov and Mamkaeva (1975) compared the ultrastructure of Aphelidium to another chytrid, Olpidium brassicae, in detail. He concluded that Aphelidium is much more like Olpidium and other chytrids than like Pseudospora and the flagellated protozoans. He notes that Olpidium differs from Aphelidium in having no stiletto, no phagocytosis and more mitochondria. Olpidium is also characterized by formation of an exit tube

for zoospore discharge, which Aphelidium lacks. Considering that the stiletto and phagocytosis may not be definitive characters for Aphelidium, these two genera are quite similar. Gromov and Mamkaeva (1975) proposed either the inclusion of Aphelidium in the Olpidiaceae or placement in a separate group intermediate between flagellates and chytrids.

The primary objection to placing Aphelidium in the Olpidiaceae has been the possibility that the similarity of these organisms is the result of convergent evolution. While it is well known that endoparasitic organisms from diverse taxa share the trend to reductionism -- often to the point of retaining only structures related to food processing and reproduction (Ricklefs, 1979), -- this is not sufficient evidence that these organisms are of different origin. It appears that it is mainly tradition that has kept these genera in different Kingdoms. After all, the taxonomy of other monads and chytrids is based exclusively on their morphology, not on speculation regarding their evolutionary past. Grouping these morphologically similar taxa together is more consistent with our treatment of other groups and the current state of our knowledge.

It is possible that the taxonomic status of these endoparasites can not be resolved on the basis of

morphological traits alone. The classical traits used to separate fungi and protozoa, e.g. presence of a cell wall, become obscured by the unicellular, endoparasitic habit. More data on the ultrastructure of the Aphelidium zoospore would be helpful. In addition to morphological data, physiological and biochemical data such as wall chemistry, food storage products, nutrient requirements and other metabolic pathways may be needed to understand the evolutionary relationships between these organisms.

In summary, Aphelidium chlorococcarum and Rozella allomycis are very similar morphologically. Differences are: the resting spore wall texture, whether the host is algal or fungal, the presence of orange waste products, and minor aspects of zoospore ultrastructure. More work on the zoospore ultrastructure of Aphelidium is needed to determine whether these genera ought to be combined. In the meantime, Aphelidium, Rozella, and Olpidium ought to be in the same family. They fit the criteria for the Olpidiceae, yet they resemble one another more closely than other Olpidiaceous genera. Rather than establish a new family for these endoparasites on the basis of incomplete evidence, I propose that Aphelidium be reclassified as a member of the Olpidiaceae in the Chytridiales.

Plate I. Differential interference contrast micrographs of Aphelidium chlorococcarum. 2,500 X.

1-4. A. chlorococcarum parasitizing a lagoon strain of Scenedesmus obliquus.

1. Recently germinated, encysted zoospore.
2. Encysted zoospore with three of the four lipid globules visible.
3. Uninfected host cell on the right. Left cell is a previously parasitized host cell with an attached, ungerminated, encysted zoospore that has not penetrated the host cell. Three of the four lipid globules are visible in the ungerminated cyst.
4. Two parasitized host cells after zoospore discharge. An exit tube is visible on the left cell. The cell on the right contains a waste globule in a vacuole.

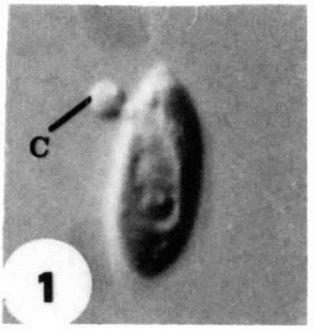
5-9. A. chlorococcarum parasitizing a lagoon strain of Scenedesmus acuminatus.

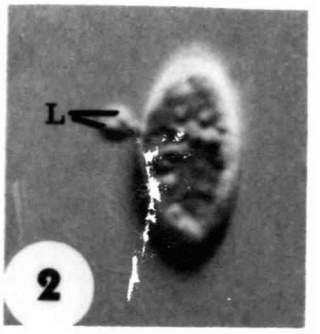
5. Germination of an encysted zoospore. One of the lipid globules is visible in the germ tube.
6. Empty encysted zoospore wall after germination.
7. Empty encysted zoospore wall on the middle cell. The intracellular parasite is visible in this host cell.
8. Two parasitized cells. Left cell is partially digested by the intracellular parasite. Right cell shows an immature sporangium with scattered lipid globules and a waste globule in a vacuole.
9. Mature sporangium in the cell on the right. Lipid globules are visible in the zoospores.

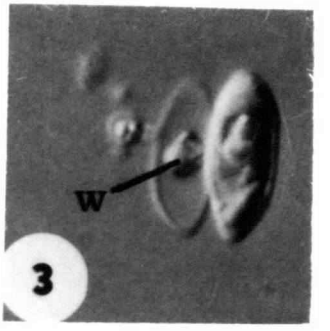
Abbreviations:

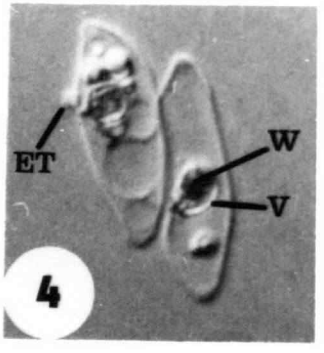
C	encysted zoospore
EC	intracellular parasite cytoplasm
ET	exit tube
L	lipid globules
V	vacuole
W	waste globules
Z	zoospore

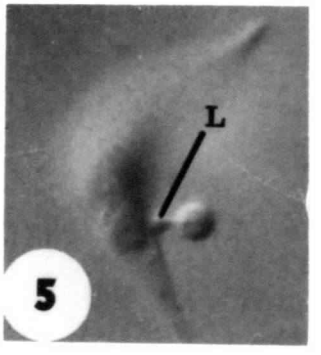
Plate I

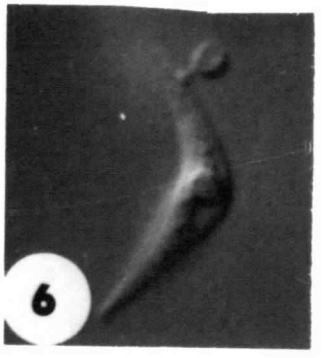


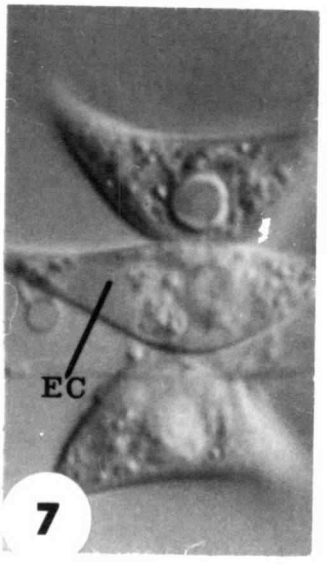


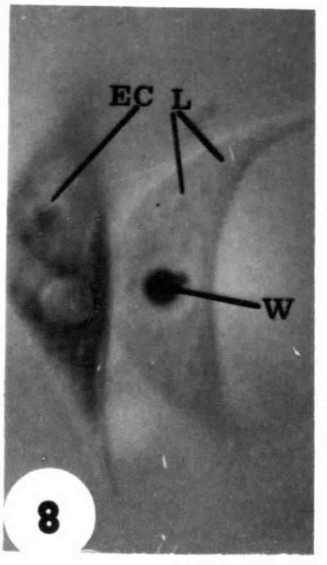












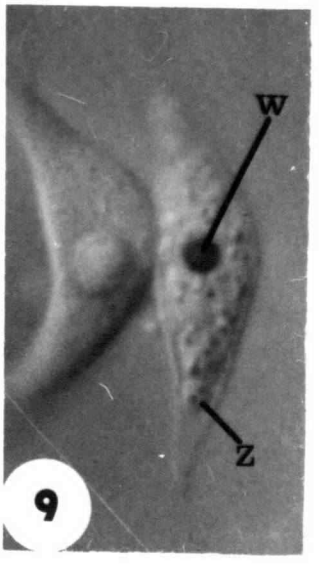


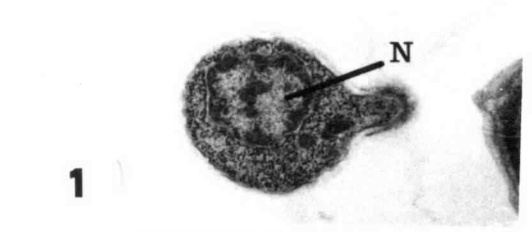
Plate II. Transmission electron micrographs of early stages of infection by Aphelidium chlorococcarum parasitizing Scenedesmus acuminatus. Gluteraldehyde-osmium fixation.

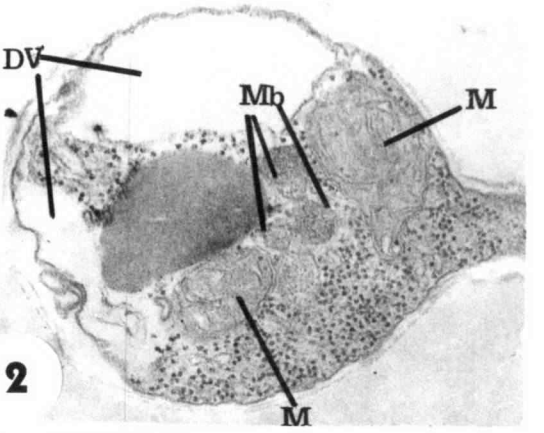
1. Ungerminated encysted zoospore. The chromatin is concentrated near the periphery of the nucleus. 15,700 X.
2. Germinated cyst with 2 mitochondria and 4 unidentified organelles that may be microbodies. 33,900 X.
3. Host cell with intracellular parasite. Visible are 5 lipid globules, 8 mitochondria, fragments of endoplasmic reticulum, and a vacuole. 15,700 X.
4. Germinated cyst. Distal vacuole is surrounded by layers of membranes. A mitochondrion and a vacuole are visible in the intracellular parasite. 17,300 X.
5. Germinated cyst with a large distal vacuole. Intracellular parasite contains 3 lipid globules, 2 mitochondria and 4 unidentified organelles -- possibly microbodies. 11,600 X.
6. Germinated cyst with a large distal vacuole. One lipid globule is in the germ tube, 3 are in the intracellular parasite. Also visible are 7 mitochondria and a vacuole. 11,100 X.

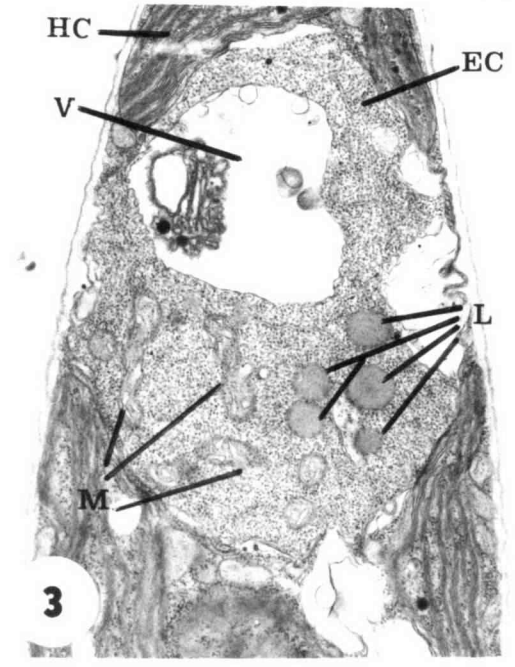
Abbreviations:

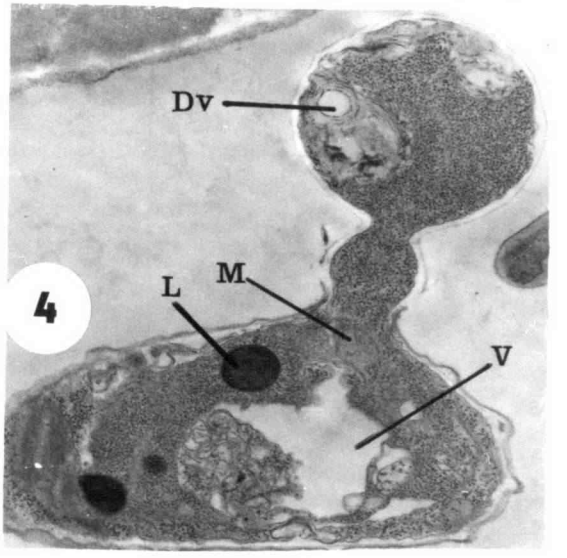
DV	distal vacuole
EC	intracellular parasite cytoplasm
HC	host cytoplasm
L	lipid globules
M	mitochondrion
Mb	microbody
N	nucleus
V	vacuole

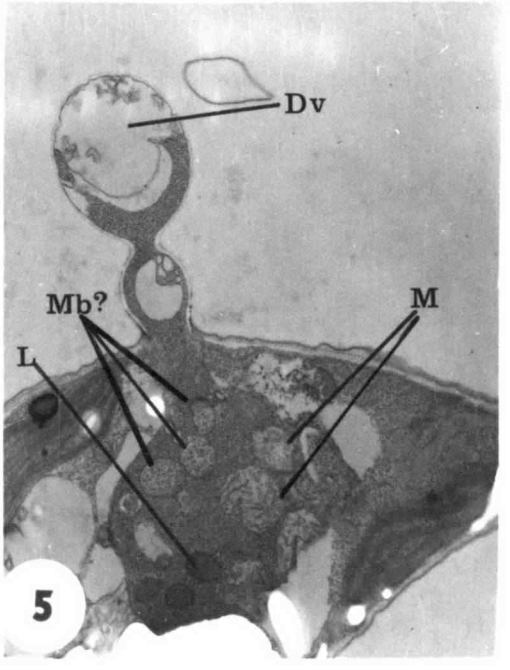
Plate II











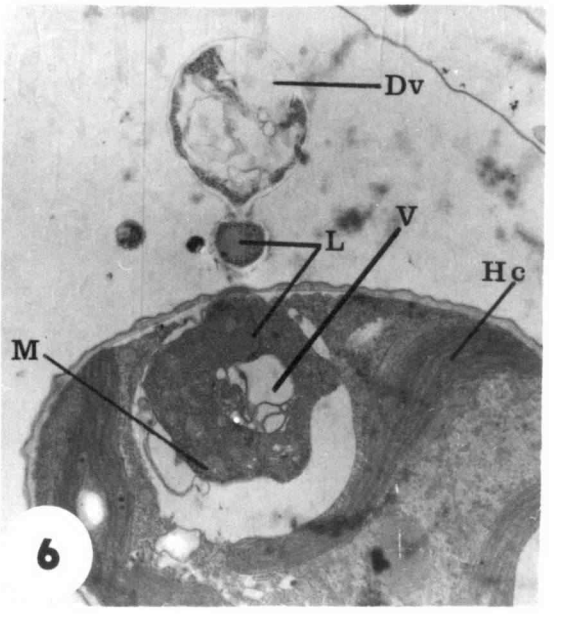


Plate III. Electron micrographs of early stages of infection by Aphelidium chlorococcarum parasitizing Scenedesmus armatus (III-1&2) and Scenedesmus obliquus UT 72 (III-3 to 6). Gluteraldehyde-osmium fixation.

1. Ungerminated encysted zoospore attached to dead host wall contains a nucleus, lipid globules, and an unidentified organelle, possibly a microbody. Also see reconstruction of serial sections in Fig. 22-R. 44,000 X.
2. Encysted zoospore attached to a dead host wall. Visible are the nucleus, distal vacuole and an unidentified organelle, possibly a microbody. 29,000 X.
3. Ungerminated encysted zoospore. The nucleus and a cluster of lipid globules around the distal vacuole are visible. Also see reconstruction of serial sections in Fig. 22-S.
4. Intracellular parasite. Visible are a mitochondrion and a vacuole. 21,000 X.

5&6. Germ tube wall terminates just inside of the host wall. 13,000 X and 13,300 X respectively.

Abbreviations:

Dv	distal vacuole
Hc	host cytoplasm
Hw	host wall
Iw	germ tube wall
L	lipid globules
M	mitochondrion
Mb	microbody
N	nucleus
V	vacuole

Plate III

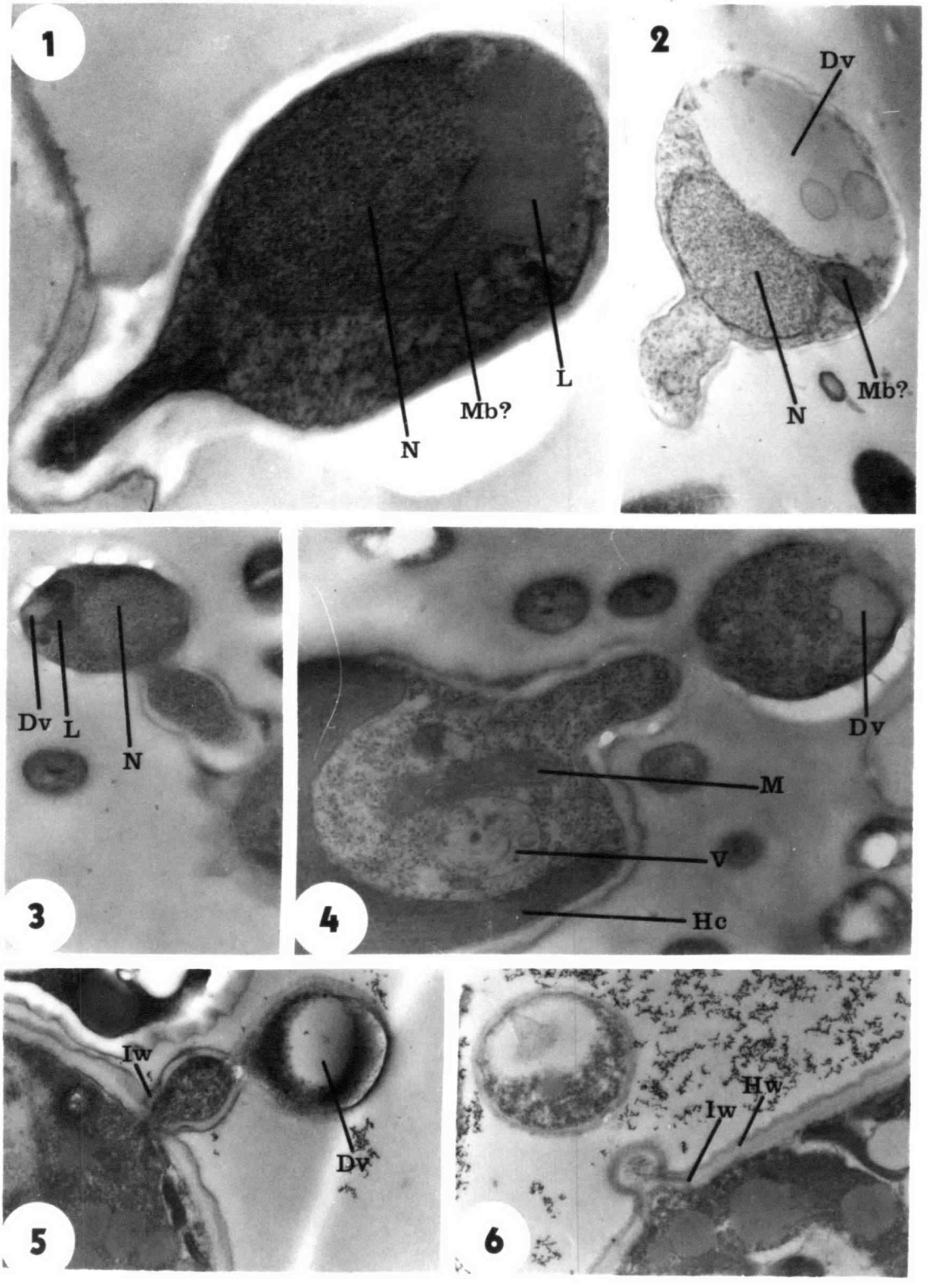


Plate IV. Electron micrograph of a zoosporangium of Aphelidium chlorococcarum parasitizing Scenedesmus acuminatus. Section through a zoosporangium containing 6 amoeboid zoospores. Lipid globules, mitochondria, nucleus and flagella are visible. 34,800 X. Gluteraldehyde - osmium fixation.

Abbreviations:

F	flagella
HW	host wall
L	lipid globules
M	mitochondrion
N	nucleus

Plate IV

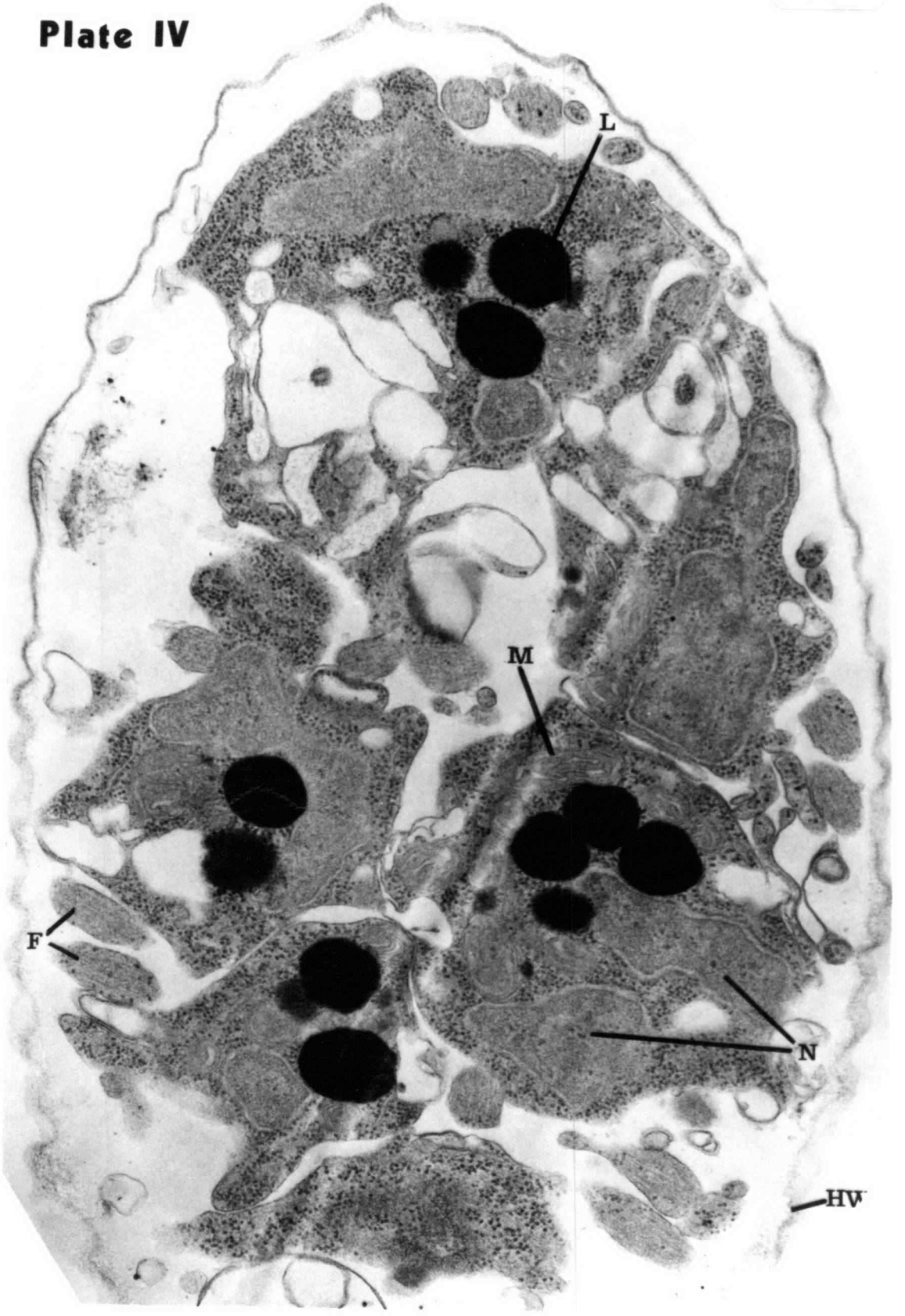


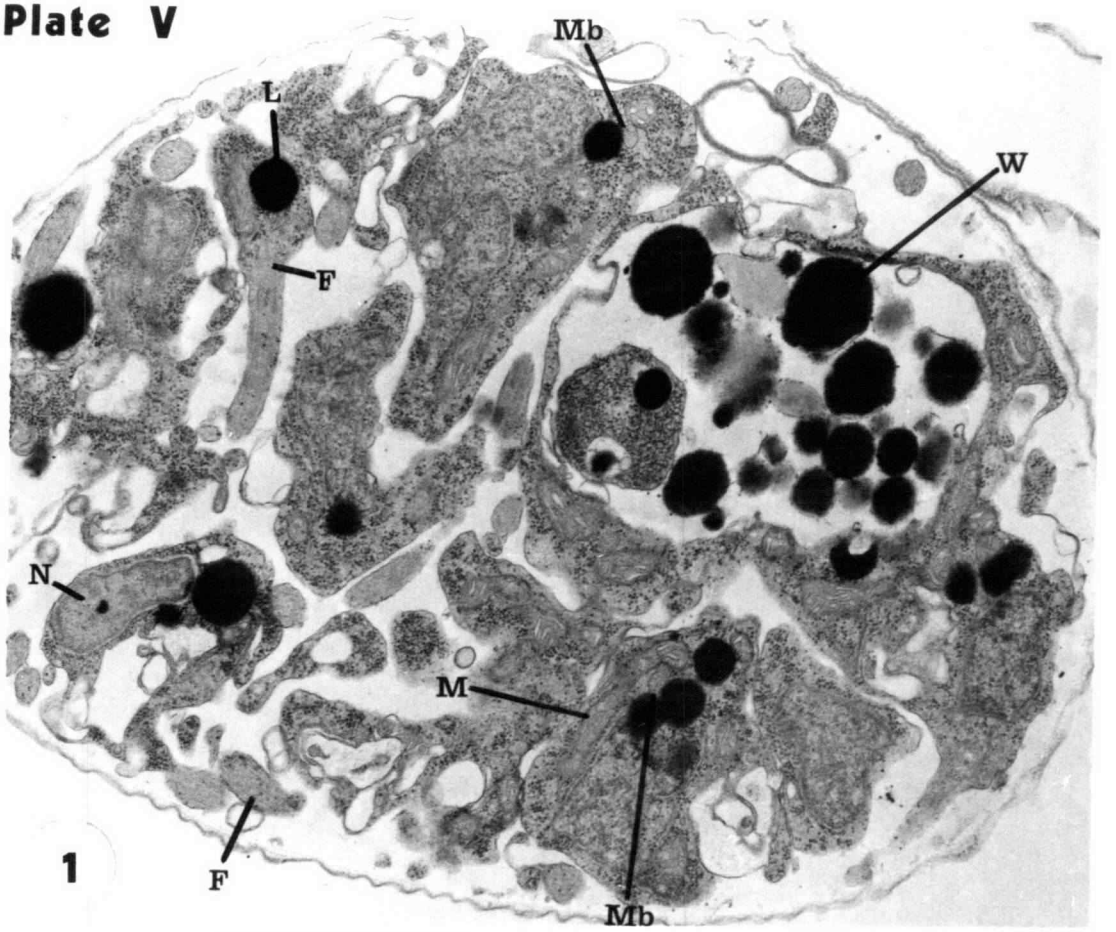
Plate V. Electron micrographs of Aphelidium chlorococcarum parasitizing Scenedesmus acuminatus: zoosporangium and dead host cells. Gluteraldehyde-osmium fixation.

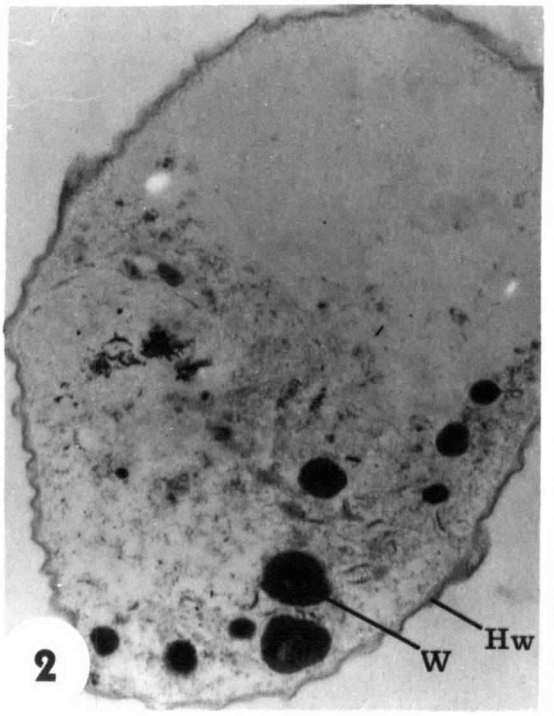
1. Section through a zoosporangium containing 8 zoospores and a large vacuole. Lipid globules, mitochondria, nucleus, flagella and unidentified organelles -- possibly microbodies are visible. "F" indicates a longitudinal section through a flagellum at the point of insertion. 17,300 X.
2. Parasitized host wall after zoospore discharge. Visible are waste globules and unidentified cytoplasmic remains. 16,700 X.
3. Parasitized host wall after zoospore discharge. Only waste globules remain. 11,000 X.

Abbreviations:

F	flagella
HW	host wall
L	lipid globules
M	mitochondrion
Mb	microbody
N	nucleus
W	waste globules

Plate V





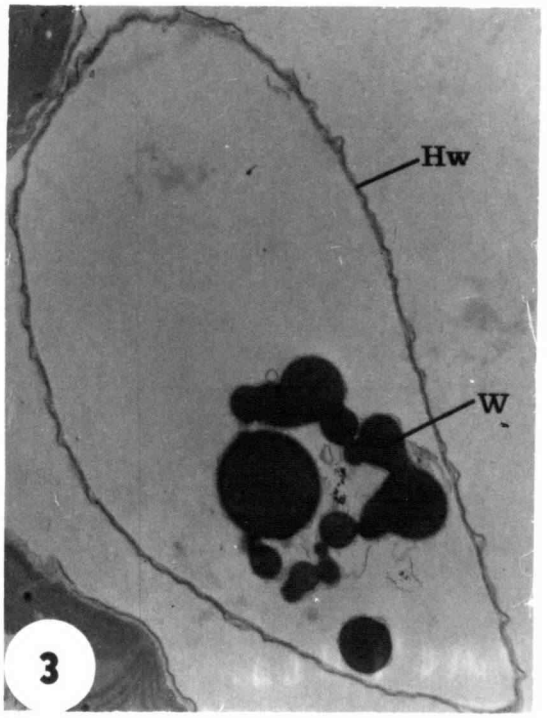


Plate VI. Serial sections through an Aphelidium chlorococcarum zoosporangium in a cell of Scenedesmus obliquus UT72. Gluteraldehyde-osmium fixation.

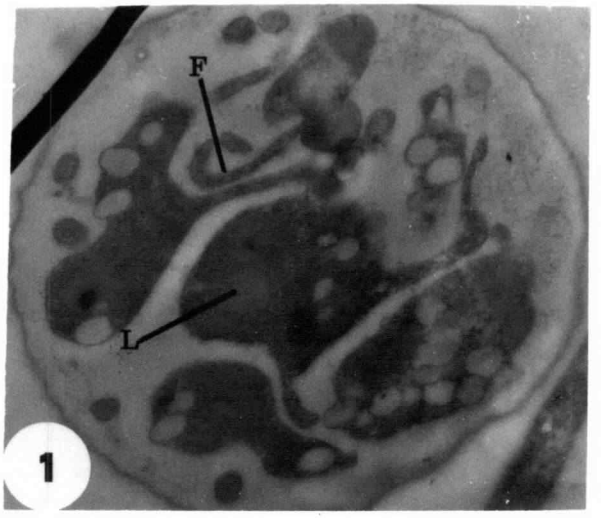
1. Section 1 16,500 X.
2. Section 3 16,500 X.
3. Section 4 15,500 X.
4. Section 10 11,600 X.
5. Section 11 11,600 X.
6. Composite drawing of sections in VI-1,2 & 3. 13,400 x.

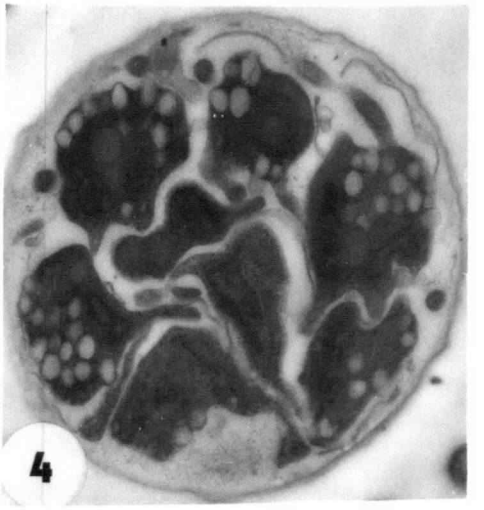
Black = lipid globules (L)
Stipled = flagella (F)
Striped = nucleus (N)

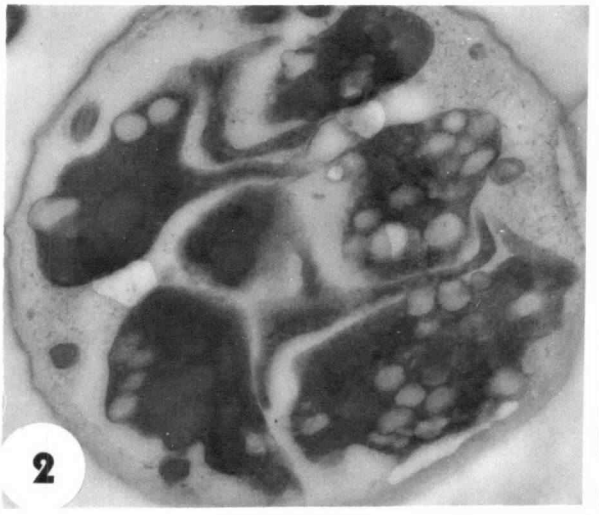
Abbreviations:

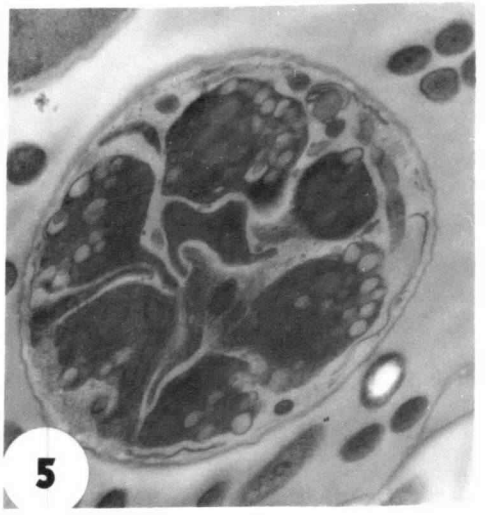
F flagella
L lipid globule
N nucleus

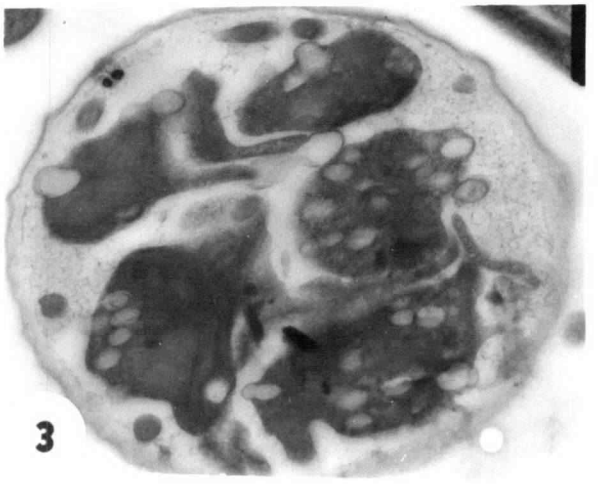
Plate VI











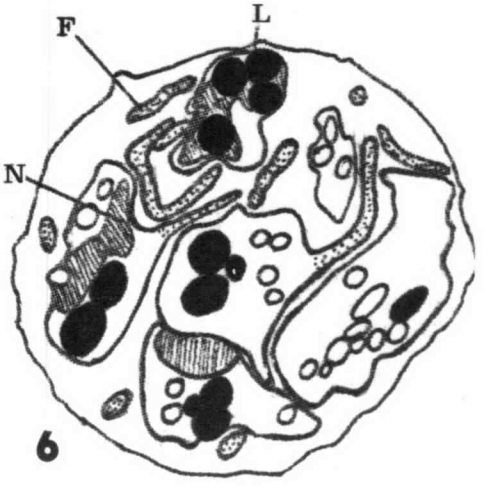


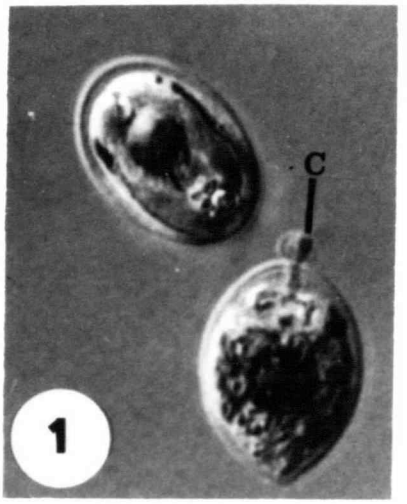
Plate VII. Differential interference contrast micrographs of *Rhizophydium* sp. infecting *Chlamydomonas ovata*. 2,400 X.

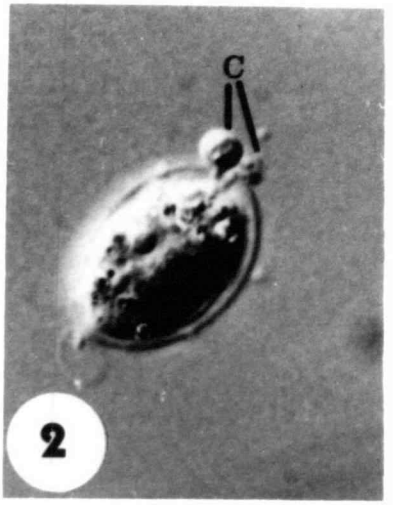
1. Uninfected *C. ovata* cell above. Germinated encysted zoospore on the lower cell.
2. Two encysted zoospores on *C. ovata*.
3&4. Immature sporangia.
5. Large immature sporangium. Rhizoids are visible in the cytoplasm of *C. ovata*.
6. Mature sporangium with 7 zoospores visible.

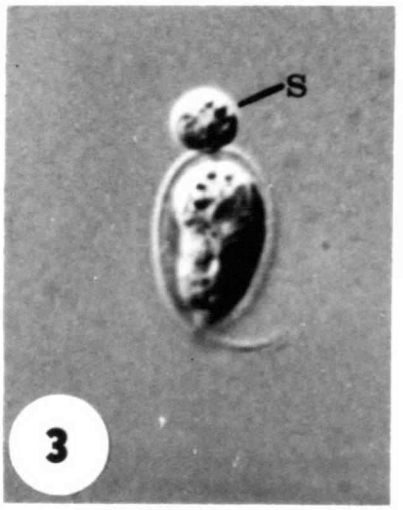
Abbreviations:

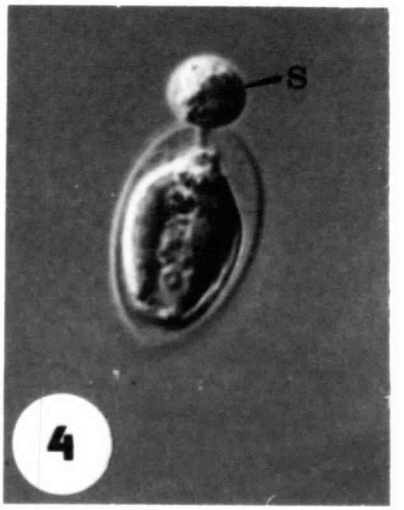
C - encysted zoospore
R - rhizoids
S - sporangium
Z - zoospore

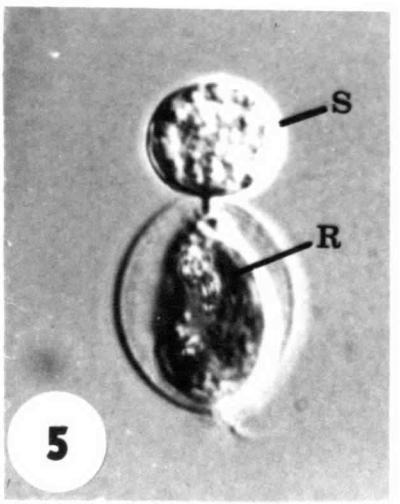
Plate VII

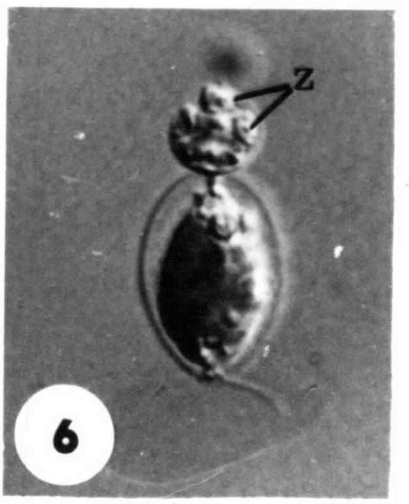












DISCUSSION

Impact of *Aphelidium chlorococcarum* on Algae

Although the impact of parasitism on the abundance of the host species cannot be conclusively demonstrated from field observations, it seems reasonable to infer that parasites have contributed to the decline of a host if the following criteria are met:

1) Parasites attack a rapidly growing host population.
2) Parasites infect apparently healthy host cells.
3) The host population declines substantially at the time of infestation or shortly afterward, but uninfected species do not decline.
4) The fraction of dead, parasitized host cells rises during the decline of the host.
5) The host population resumes growth after the parasite population declines.

Aphelidium chlorococcarum was the most common parasite in the lagoon. It was also the only one that was abundant enough to be able to assess its impact on host populations. *Aphelidium* was observed during most months of the two year study, increasing to zoospore densities above 10^3 cells/ml during the summer and fall. Furthermore, it infected a broad range of hosts mainly in the Chlorococcales. Consequently, *Aphelidium*

was potentially an important factor in the abundance of algal species in the lagoon.

The criteria above are the basis for the following evaluation of the impact of A. chlorococcarum on the three host species subject to the most severe parasitism in the sewage lagoon: Scenedesmus obliquus, S. armatus and Ankistrodesmus falcatus. Other species were also severely parasitized, but the host and parasite population densities were too low to estimate abundance accurately enough to assess the impact of parasitism.

Neither of the most severe infections of Scenedesmus obliquus (26% and 25%) during the two year study appeared to reduce the population of S. obliquus significantly. In 1979, when 26% of the population was infected, the host cell density did not decrease until two weeks later. The decline was not substantial and no parasites or dead, parasitized host cells were observed on the date of the decline. Thus, this decline was probably unrelated to the epidemic.

In 1980, when 25% of the S. obliquus population became parasitized, a very severe decline in the host population occurred -- from 130,000 to 1900 cells/ml. However, the decline coincided with a sharp decline in nearly all of the algal species whether or not they were parasitized. Two days before this decline, a

nearby lumber mill burned and the lagoon was covered with ash from the fire. During this period, the weather was optimal for phytoplankton growth. Since no other equally severe decline of all species was observed during favorable weather for growth of algae, it is probable that the fire was a factor in both the decrease of phytoplankton density as well as the severe parasitism that occurred on S. armatus and Ankistrodesmus falcatus on the same date.

Infection of Scenedesmus armatus was more frequent and severe than infection of any other algal species in the lagoon. The immediate effect of the most severe infections (40% to 74%) was a sharp decrease in the number of host cells for as long as a month and an increase in the fraction of dead cells. The greater frequency and severity of infections of S. armatus may be a result of the inclusion of several species in this taxon. Perhaps each of the actual species only suffered epidemics once or twice a year. Whether the species included in S. armatus are differentially susceptible to Aphelidium is unknown since only the actual species, S. armatus, was grown in laboratory culture and served as a host for Aphelidium chlorococcarum.

In 1979, five separate episodes of severe parasitism of S. armatus occurred. All of these were asso-

ciated with declines in the host population, although these were not significant at the relatively low host cell density. A severe infection in July (74% and 65% on successive weeks) had more impact on S. armatus than any other episode of parasitism observed in this study. The host population was reduced for four weeks and as many as 64% of the cells were dead. The population did not resume growth until two weeks after dead host cells were last observed.

In 1980, S. armatus was much more abundant than in the previous year. There were four episodes of severe parasitism, and each time the host population decreased during the epidemic. Substantial declines of S. armatus occurred in July, August and October when infections were 56%, 53% and 42% respectively. On the same dates, many dead cells were observed (23% to 37%). Between the August and October epidemics, low fractions of host cells were infected even though the density of S. armatus was continuously above 10^5 cells/ml.

Ankistrodesmus falcatus was severely parasitized three times in 1980. The July epidemic had the most impact on the host population. This epidemic lasted for four weeks with as many as 100% of the cells infected and 37% dead, and the host population density fell from 19,000 to zero cells/ml during this interval. The Ankistrodesmus population declined to zero and the

total phytoplankton density decreased the same week that the lumber mill burned. But before the fire, a severe decline in the host population had already occurred. After the fire, the Ankistrodesmus population resumed growth and parasites were rare until October.

In summary, the impact of parasitism by Aphelidium chlorococcarum on the host populations was generally minor. Aphelidium chlorococcarum occurred throughout the year, but usually less than 10% of the potential host populations were infected. Infections more severe than 50% typically occurred only once or twice a year on each host species. S. armatus was severely infected more frequently. Episodes of severe parasitism occurred five times each year. Perhaps this was because S. armatus actually included three species. Most severe infections did not last more than a week and as the number of parasitized cells declined, the host population resumed growth. Thus even severe parasitism caused only a temporary decline in host populations. There was no evidence of parasitism completely eliminating a host species from the assemblage of algae.

There was no correlation ($r = -0.26$) between a higher percentage of infection and the magnitude of

decline of the host population. In several cases, the host population even increased substantially during the week of a severe infection. For example, S. armatus increased by 90,000 cells/ml during week 80 when 32% of the population was infected. The absence of a correlation between severe parasitism and greater declines in host populations may be due to counting error or gaps in available data resulting from the sampling strategy. The most severe decline observed lasted a month. This occurred when 74% of the S. armatus population was infected. In most instances, infections greater than 10% were associated with some decline in the host population regardless of the magnitude of the decline.

The pattern of chronic low levels of infection by Aphelidium chlorococcarum occasionally interspersed by sporadic epidemics is similar to the field observations of parasitic chytrids (Canter and Lund, 1969). A similar pattern also occurred in the infection of Schizothrix calcicola by an LPP cyanophage in continuous culture (Cannon et al., 1976). After introduction of LPP cyanophages into a chemostat, and initial high rates of infection, the relative abundance of the host and parasite stabilized so that a constant low fraction of the host population was parasitized. All of the host cells isolated after the epidemic were resistant to viral infection. One explanation for this pattern

is that the original host population was a mixture of susceptible and resistant strains. The initial infection quickly reduced the number of susceptible host cells to low levels. As the number of parasites and susceptible host cells was very low, the chance of parasites encountering every host cell was diminished, so some susceptible host cells survived. Similarly in the lagoon, when susceptible host cells are rare after an epidemic, the frequency of encounter with parasites is low so not all of the susceptible host cells are killed by parasites. A low percentage of these are infected and both the host and parasite survive. There were no obvious morphological differences in either the hosts or parasites that might relate to susceptibility or virulence. However, susceptibility differences probably exist since they are known for many host/parasite relationships (Flor, 1956). Other authors have observed susceptibility differences in strains of the hosts parasitized by chytrids (Koob, 1966; Masters, 1971c) and by Aphelidium (Gromov, 1972b; Gromov and Mamkaeva, 1970).

Impact of Parasitism on the Succession of Species in the Lagoon

Several authors have commented that the decline of a species during parasitism results in the increase of other species (Reynolds, 1973; Van Donk and Ringelberg, 1983). The three clearest instances of severe parasitism in the lagoon that were accompanied by sharp declines in the host populations were examined. If only the parasitized host species decreased, the decline was assumed to be the result of parasitism. If many uninfected algal species -- especially closely related species -- also declined on the same date, some other factor than parasitism was considered responsible for the decline.

Scenedesmus armatus was heavily parasitized (74% and 65%) in July of 1979 and declined for three weeks. This episode of parasitism was the msot severe of those observed in the lagoon study and it had the greatest impact on the host alga. During this time, the density of other species increased. These included Scenedesmus acuminatus, S. obliquus, Oscillatoria lutea and Chlamydomonas ovata. In this example, the decline of a heavily parasitized host species was accompanied by an increase in the density of other species. Severe parasitism seems to have altered the succession of species.

Scenedesmus armatus was also severely parasitized (32% and 53%) in August of 1980, and declined sharply. However, several other uninfected species (S. acuminatus, S. obliquus and Tetraëdron minimum also declined. At the same time the populations of the blue-greens -- Nostoc commune, Anacystis incerta, and Schizothrix calcicola increased. Because a shift in dominance from green algae to blue-greens occurred, some factor other than parasitism was probably involved in this case.

Severe infections of three species -- Scenedesmus armatus (56%), S. obliquus (25%) and Ankistrodesmus falcatus (33%) occurred on July 24, 1980. The total phytoplankton density in both ponds decreased dramatically on this date. Clearly the decrease was unrelated to parasitism. The weather was optimal for algal growth: hot, no precipitation for weeks, and maximum light intensity. The decline seems to have been related to the destruction of a lumber mill by fire two days before the samples were collected. The ponds were still coated with ash on the sampling date. By the week following the fire, the total phytoplankton density had apparently recovered as it had increased to the highest density observed in the two year period. Maximum densities of the infected species (S. armatus, S. obliquus and Ankistrodesmus falcatus) also occurred the week after the fire. It may be that the severe

infections of these species resulted from the ash temporarily inhibiting the growth rate of the algae more than that of Aphelidium. While the total number of host algae decreased by a magnitude of 75 times during the week before July 24, 1980, the Aphelidium population decreased only 41 times.

Only one of these epidemics supported the contention that parasitism could be important in algal species succession, and that was the most severe episode of parasitism in the lagoon. Other factors, such as weather and an influx of ash from a fire were associated with much larger declines in species populations than declines related to parasitism. Perhaps it is predictable that the impact of Aphelidium on the succession of algal species appeared to be negligible since parasitism by Aphelidium never eliminated a host species and rarely reduced the host density very much for more than a few weeks.

Overall, the impact of parasitism on algal species in the lagoon was minimal. This is predictible in the context of the coevolution of a host/parasite relationship. In theory, a well adapted obligate parasite must not eliminate its host or it cannot survive. Over time, host species develop resistance mechanisms, and parasites eventually adapt to overcome the resistance.

Thus, only host/parasite systems that allow the survival of both organisms will be successful during the course of evolution. This theory has been expressed in genetic terms by Flor (1956) in his gene-for-gene hypothesis. The theory is that for every gene in the host that determines resistance, there is a corresponding gene in the pathogen that determines a- virulence. Various combinations of these genes in host and parasite strains result in only a fraction of a host population being parasitized. One hypothesis for the minimal impact of parasitism on host species populations in the lagoon is that the host and parasite populations are mixtures of strains that vary in susceptibility and virulence. When many of the susceptible host cells have been killed, the frequency of encounter with parasites is so low that some of the susceptible host cells survive.

Environmental Factors That Favor Epidemics

Authors of previous field studies have been unable to identify parameters that precipitate epidemics of parasitism. The following discussion will consider whether changes in any of the climatic factors, properties of the aquatic environment, or biological factors examined in this study might have been related to the occurrence of episodes of severe parasitism. Severe

parasitism and epidemics are arbitrarily defined as episodes where more than 10% of a host population was infected.

Climatic factors: light, temperature, and precipitation

Several laboratory studies have shown that a minimum light intensity is required for encystment or germination of chytrid zoospores (Canter and Jaworski, 1981; Abeliovich and Dikbuck, 1977; Barr and Hickman, 1967). However, this minimum seems to be well below light intensities that commonly occur in the field. Seasonal fluctuations in light intensity were unrelated to the occurrence of epidemics in this study. Infections more severe than 10% were observed both in the fall, when light intensities varied from 100 to 300 langleys/day, and in the summer (300 to 600 langleys/day). Thus, epidemics occurred over the entire range of light intensities observed in the lagoon.

Some authors suspected that temperature changes triggered chytrid epidemics (Pongratz, 1966; Fott, 1967; Masters, 1971d). In contrast, Canter and Lund (1948) found no relationship between increased infection rates and temperature fluctuations. In the sewage lagoon, the episodes of severe infection by Aphelidium also seemed unrelated to temperature changes. Severe

infections occurred at water temperatures ranging from 4°C to 21°C. Nor was there any relationship between the direction of temperature change and epidemics. There is laboratory evidence that very low temperatures (below 4°C) inhibit chytrid activity more than they inhibit the growth of the host alga (Van Donk and Ringleberg, 1983). However, the temperature of the lagoon was rarely as cold as 4°C. Therefore, it seems unlikely that temperature was a factor in the occurrence of severe parasitism in the lagoon.

While light intensity and temperature seemed not to trigger epidemics in the lagoon, precipitation did appear to be important. Four out of five of the major epidemic periods observed in the lagoon were associated with increased precipitation. These episodes are examined in detail below.

The only major epidemic that was not associated with increased precipitation began in June of 1979. Infections greater than 10% occurred on at least one of the host species each week for seven weeks. Three weeks prior to the date of infection increase, precipitation decreased suddenly and remained very low (less than 0.25 cm/day) throughout the epidemic.

There was a remarkable correlation between two episodes of severe infection and increased precipita-

tion in the fall of 1979. Dry weather preceded the first epidemic in October. However, a week after the October epidemic began, precipitation increased, culminating at 1.78 cm/day in the third week of the epidemic. Increased precipitation did not initiate but may have intensified this epidemic. When dry weather resumed, the infection fell below 10%, although Aphelidium zoospores were still abundant. Precipitation increased again, and was followed by another epidemic at the end of November, four weeks after the October epidemic. The November epidemic coincided with a period of maximum precipitation (1.27 cm/day), and as precipitation decreased the epidemic ended.

A two month period of severe infections began at the end of June, 1980. The epidemic was preceded by five weeks of dry weather (precipitation less than 0.25 cm/day) then a week of very heavy rainfall (1.27 cm/day). One week later, the severity of infection increased. Although precipitation decreased during the epidemic, severe infections continued for two months during dry weather. In this instance, only the beginning of the epidemic was associated with heavy rainfall.

Three weeks of severe parasitism began in October of 1980. Precipitation was negligible from July until one week before the epidemic when rainfall increased to

0.51 cm/day. The following week was dry, then several weeks of precipitation began. The epidemic ceased before precipitation declined again. Precipitation appeared to trigger this epidemic.

Epidemics in the fall were associated with periods of increased precipitation. Epidemics each summer occurred in dry weather, but heavy rainfall preceded the beginning of the epidemic in the summer of 1980. It is clear that severe parasitism does not require increased precipitation. However, heavy rainfall does seem to be associated with many epidemics. This may be the result of slower growth of the host algae in rainy weather relative to growth of the parasites.

Properties of the aquatic environment: pH, BOD, Suspended Solids, and Nutrients

None of the aquatic environmental parameters were measured frequently enough to yield definite conclusions about their correlation with episodes of severe infection. Nutrient concentrations were measured on only six dates. Suspended solids, pH, and BOD were only measured once each month. Monthly samples of the pH and BOD are particularly inadequate considering the wide range of values that occur daily in sewage lagoons. Nevertheless, the data on these variables in

Pond II will be examined for preliminary indications of any relationship with the occurrence of epidemics.

In general, nutrients could effect the occurrence of epidemics by limiting or enhancing the growth of a host and/or parasite thus altering their relative growth rates. Nutrient limitation is widely regarded as an important factor in the abundance of phytoplankton in lakes. Van Donk and Ringelberg (1983) documented the replacement of Asterionella by other diatom species. They believed this was the result of parasitism interacting with competition by the algae for nutrients. Nutrient limitation might also increase the susceptibility of a host to parasitism by stressing the host. However, nutrient limitation probably was not a factor in the lagoon since nitrate, phosphate and carbonate concentrations were well above limiting levels for algal growth (Wetzel, 1975; Vollenweider, 1968)

It is possible that the concentrations of nutrients, while not limiting for algal growth, could have other effects on the relative growth rates of the host and parasite that result in epidemics. A preliminary test of this hypothesis was made by comparing the concentrations of major nutrients required for algal growth during and between epidemics in the lagoon. Half of the six nutrient measurements in 1980 were from samples collected during epidemics. These were the

first two and the last of the six sampling dates. The remainder of the samples were collected when host and parasite populations were abundant but infection rates were below 10%. Of the nutrients measured, the forms most readily available to algae for growth are ammonium, nitrate and nitrite, dissolved orthophosphate and dissolved inorganic carbon. Orthophosphate and nitrate were both lower during epidemics than when infections were less severe (Fig. 5). These data are insufficient to conclude whether nutrient concentration was related to the occurrence of epidemics.

Aside from mineral nutrients required for algal growth, many other substances, especially organic compounds, are found in sewage ponds. Any change in the chemistry of the lagoon that affected the algal hosts could potentially influence the rate of parasitism. Changes in the concentration of organic substrates in the lagoon could also affect growth of some of the algal species that are capable of heterotrophic nutrition, e.g. Chlamydomonas assimilates acetate. Extracellular metabolites of certain species may enhance or inhibit growth of other species (Keating, 1976). Furthermore, algal species vary in their tolerance to high concentrations of nutrients and in their requirements for minor nutrients (Wetzel, 1975).

There is preliminary evidence that eutrophic water favors increased parasitism. Shane et al. (1972) and Safferman and Morris (1967) found more phycoviruses in water with increased sewage content. Canter and Lund (1953) found more chytrid parasites in the more eutrophic lakes in England. Furthermore, in preliminary laboratory tests, I found that growth of Aphelidium chlorococcarum on Scenedesmus species in sterile sewage lagoon water was inhibited if the lagoon water was diluted more than 50% with distilled water. These observations raise the question whether some components of sewage either enhance parasite growth or are detrimental to growth of the algal hosts, resulting in an increase in parasitism.

The BOD (biochemical oxygen demand) is a measure of the relative amount of oxygen required by organisms in water samples to metabolize organic matter in the sample. Thus, it is a function of both the amount of organic matter and the community composition and the number of organisms. While it is not a measure of the DO (dissolved oxygen concentration) of the water, there is a relationship between the two measurements. At night when photosynthetic oxygenation of water ceases, water with a high BOD is more likely to become anaerobic. There is some evidence that dissolved oxygen concentration has an influence on the infection rates

of algae by chytrids. Canter and Lund (1948) found that aeration of cultures increased the percentage of infection. Abeliovich and Dikbuck (1977) found that when dissolved oxygen was either near saturation or anaerobic levels, a Chytridium species was unable to infect Scenedesmus obliquus. They believed that oxygen concentration was the fundamental factor influencing infection rates. They hypothesized that epidemics in sewage lagoons would be favored by lower BOD's by preventing anaerobic conditions from developing at night.

In the lagoon, BOD values during months when severe parasitism occurred were compared to those values when it did not occur. BOD was low (less than 10 mg/l) during four of the seven months when severe parasitism occurred. But there was no correlation between BOD and periods of severe parasitism. Given the wide fluctuations in BOD that were observed in the sewage lagoon, more data is needed before concluding whether BOD or DO are related to the occurrence of epidemics.

Suspended solids refers to the dry weight of the residue of a sample retained by a glass fiber filter. The residue is composed of particulate matter, bacteria, algae, fungi and other organisms. Algae are a

large component of the suspended solids in the lagoon. Since severe parasitism by Aphelidium occurs when the total phytoplankton and the host species are more abundant, one might expect to find more severe infections when suspended solids are greater. The range of suspended solids values in Pond II was from 10 to 80 mg/l. Episodes of severe parasitism did occur only when the suspended solids value was high (greater than 30 mg/l) as predicted. This probably reflects the increased likelihood of epidemics occurring when host species are most abundant.

None of the authors who have examined changes in pH relative to increased infections (Paterson, 1960; Masters, 1971d; Barr and Hickman, 1967) have found any relationship between the two parameters. The pH of sewage lagoons containing large algal populations typically fluctuates as widely in response to diurnal photosynthetic activity as it does seasonally. Partial compensation for these diurnal fluctuations was probably achieved by sampling at approximately midday. The pH values in the lagoon during episodes of more severe parasitism varied from 8 to 9. This was the same range of pH values observed when no epidemics occurred except that in the winter pH was sometimes as low as 7. There is probably no direct relationship between pH and epidemics in the lagoon.

Biological Factors: total phytoplankton density, host density, host growth rate, host susceptibility and hyperparasitism

Biological factors other than parasite activity may also be important in the initiation of epidemics. Those monitored in this study included: host density, rapid changes in host population density, and total phytoplankton density. Other factors that were not included in this project, but are known to be important from other investigations will be discussed briefly. These are host susceptibility, parasite virulence and hyperparasitism.

Canter and Lund (1969) and Masters (1971c) concluded that an abundant host population favored chytrid epidemics more than any other factor they studied. Soeder and Maiweg (1969) observed the same tendency in outdoor mass cultures. The cultures were relatively free of parasites until a susceptible host strain became abundant. Then severe parasitism developed. Similarly, in the sewage lagoon the severity of parasitism by Aphelidium increased when host populations became abundant. Most of the year, encysted zoospores were observed on less than 10% of the host population. When the total number of host cells of all the species parasitized by Aphelidium increased above 10^4 cells/ml,

then more severe infections occurred. Lund's (1957) hypothesis that the greater proximity of host cells in denser populations increases the probability of parasite zoospores encountering a host seems a reasonable explanation of this phenomenon. His notion is consistent with observations that agricultural crops are subject to more severe parasitism when grown as dense monocultures than when different crops are grown in alternate rows. The latter is thought to interrupt the spread of disease by increasing the distance between hosts. Host density alone is clearly not sufficient to explain the occurrence of epidemics. Host populations in the lagoon were often abundant and relatively free of parasites.

The growth rate of the host population may well influence the onset of epidemics. Masters (1971d) hypothesized that rapidly growing hosts produce exudates that stimulate parasite growth. Or, as Reynolds (1973) proposed, if a severe infection occurs near the beginning of the increase of a host, a more severe infection may result. In the lagoon, many of the severe infections on S. obliquus and S. armatus occurred when the host populations were increasing rapidly. But severe infections were found also on other host species (Actinastrum, Ankistrodesmus, Tetraëdron, and Pteromonas angulosa) during the maximum

or declining phases of population development. Most of these other species were not abundant enough to accurately estimate parasite populations. In the lagoon there seemed to be a tendency for severe parasitism to develop when host populations were increasing rapidly, but the data are inconclusive.

The relationship between the total phytoplankton density in the lagoon and episodes of severe parasitism was investigated. It is possible that a dense total phytoplankton population was more conducive to parasitism aside from the effect of host cell abundance. Episodes of severe parasitism by Aphelidium chlorococcarum were only observed when the total monthly phytoplankton population was very high (above 2×10^5 cells/ml). Severe infections were not observed in four of the months when the total phytoplankton density was above 2×10^5 cells/ml. These months were April and August of 1979 and September and November of 1980. In April (1979) the phytoplankton was composed mainly of species apparently not susceptible to infection by Aphelidium. In August (1979) the population of potential host species was high but for some reason Aphelidium zoospores were rare. In September and November of 1980 there were plenty of potential host species and Aphelidium zoospores but less than 10% of the host

population was infected, except in early November. Since in three of these months the potential host population was high at the same time as the total phytoplankton density, it is not possible to evaluate these factors separately. Clearly a dense total phytoplankton population combined with abundant host cells does not necessarily result in severe parasitism.

Other factors that were not studied in this project but may be important are host susceptibility, parasite virulence and hyperparasitism. In the literature review evidence was presented that strains of hosts vary in their susceptibility to parasitism. It may be that the percentage of infection observed reflects the fraction of susceptible individuals in an algal species population. While there is no evidence that Aphelidium species differ in virulence, this phenomenon is known to other parasites.

Hyperparasitism of Aphelidium is another biological factor that could influence the severity of infections. Schnepf et al. (1971) found evidence of hyperparasitism. A virus infected Aphelidium as the Aphelidium in turn parasitized Scenedesmus. It may be that as Aphelidium becomes more abundant it is then more susceptible to viral infection and this terminates an Aphelidium epidemic. Of course none of these factors were observable with the methods employed in this

study so it is not known to what extent they were important in the occurrence of epidemics in the lagoon.

Conclusions

1. Aphelidium chlorococcarum was the most common parasite of algae in the sewage lagoon. Chronic low levels of infection by Aphelidium chlorococcarum were typical during most months of the year.
2. Aphelidium chlorococcarum infected several genera of algae. All but one of these were members of the Chlorococcales.
3. Severe infections by Aphelidium chlorococcarum typically reduced the density of the host population for only a brief period. The most severe infection (74%) was associated with a decline in Scenedesmus armatus for a month.
4. Severe infections generally occurred only once or twice a year on each host species, except for S. armatus which suffered severe parasitism ten times during the two year study.
5. There was no evidence of parasitism eliminating a host species from the phytoplankton population.
6. Severe infections often resulted in a decline in the host population but the percentage of infection was not correlated with the magnitude of the decline.
7. The succession of algal species was influenced by parasitism only in the most severe (74%) of the

infections observed. In other epidemics associated with sharp declines in the host population, the decline was associated with unfavorable weather or an influx of ash from a fire, rather than parasitism.

8. The limited impact of Aphelidium chlorococcarum in the lagoon is consistent with the concept of the coevolution of hosts and parasites in a balanced ecosystem. They coexist and epidemics are rare as long as the system is not perturbed.

9. An effort was made to correlate the following environmental factors with the occurrence of epidemics.

a. Climatic factors: The range of light intensities and temperatures observed in the lagoon are apparently compatible with growth of Aphelidium but are unrelated to the occurrence of epidemics. Precipitation was associated with four of five of the major epidemics of Aphelidium. Increased precipitation appeared to favor the occurrence of epidemics.

b. Aquatic environmental factors: Nutrients were not limiting in the lagoon, but other nutrient related factors may be important in the occurrence of epidemics. There was no apparent relationship between the major nutrients, BOD or pH and the occurrence

of epidemics. These data were gathered monthly so only preliminary conclusions may be drawn.

c. Biological factors: The density of the host was more important than any of the other parameters in the occurrence of epidemics. Severe infections increased generally when the suspended solids was greater than 30 mg/l and the host density was greater than $(10)^4$ cells/ml. Severe infections do not only occur when the host density is high. Other factors are apparently important. The growth rate of the host population may be a factor in the onset of severe infections. There was a tendency for epidemics to occur more often as the host population was increasing or near the host maximum. Severe parasitism was only observed when the total phytoplankton density was above 2×10^5 cells/ml.

Recommendations for Control of Parasitism in Large-Scale Cultures of Algae Grown in Sewage

One of the problems encountered in the large-scale culture of algae for food is destruction of the culture by parasites. Control of parasites of any agricultural crop is often achieved through a variety of approaches. These generally include selection of resistant strains of the host (especially nutrient concentrations), chemical or biological control of the parasites, and study of the life history of the parasite. Except for the extensive study of the nutrient requirements of some species of algae, most of this work remains to be done.

This and other investigations suggest that control of parasitism by chytrids and Aphelidium in cultures of algae in sewage might be achieved by several methods.

Select appropriate host species

1) Select species and strains of algae that are resistant to parasitism. Scenedesmus appears particularly susceptible to parasitism by several chytrids as well as Aphelidium, so may be a poor choice.
2) Harvest algal cells frequently to prevent cultures from becoming very dense. In the

sewage lagoon, parasitism was less severe when the host density was below 10^4 cells/ml.

3) Culture of several host species simultaneously might minimize the likelihood of severe parasitism as well as reduce the chance of parasites encountering a particular species of host. In the sewage lagoon, severe parasitism did not occur if the total cell density was less than 10^5 cells/ml, and the suspended solids value was below 30 mg/liter.

Maintain optimal culture conditions

1) Establish cultures in a favorable climate for algal growth. High temperatures and light intensities are generally preferable.
2) Maintain optimal concentrations of the nutrients required for growth of the algae.
3) Determine an optimal influent rate of sewage into the culture to minimize parasitism and optimize growth of algae. Concentrated sewage may favor parasitism.
4) Maintain dissolved oxygen concentrations that inhibit chytrid infections. There is evidence that either saturation or anaerobic conditions inhibit growth of some chytrid species.

Control parasitism biologically or chemically

1) Introduce viral or other hyperparasites of chytrids or Aphelidium into the culture.
2) Add high concentrations of certain ions. Concentrations of Mg^{++} or K^{+} at 10^{-2} M have been found to inhibit infection by one species of chytrid.

The study of the control of parasites in cultures of algae is just beginning. Once appropriate host species for culture have been selected, their parasites may then be isolated in culture. This will facilitate study of life histories of the parasites as well as the genetics of the host/parasite interactions. Host/parasite cultures may also be suspended in containers in the large-scale cultures. This would enable experimentation with various methods for control of parasitism. For example, the effect of different densities of the host populations on the rate of parasitism could be tested. These approaches may serve as fruitful starting points in the search for methods of control of parasitism of algae cultured for use as a concentrated source of protein.

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APPENDICES

Appendix A. Field Notes

Field notes taken on day of sampling are coded according to the following scheme. Missing information is indicated by a dash (-).

Color of Ponds

0	clear
B	brown or tan
BG	brownish green
1	very pale green
2	pale green
3	medium green
4	dark green

Precipitation

0	none
1	light rain or showers
2	rain
3	heavy rain
4	snow

Cloud Cover

0	clear, sunny
1	partly cloudy
2	overcast
3	heavy overcast

Wind strength and direction (NE, etc.)

0	none
1	light breeze
2	windy
3	strong wind

Temperature

1	hot
2	warm
3	cold
4	frosts overnight
5	ice on lagoon (approximate thickness, inches)

Past-week: same codes indicate: precipitation/ cloud cover/temperature for the interval between sampling dates.

Date	Sample Number	Time	Temperature °C Air	Water	Color of Ponds I	II	Precip	Weather Notes: Date of Sampling Cloud Cover	Wind	Temp	Past week ppt/cc/temp	Other Notes
1/24/79	1	10 am	-	5	3	3	1	2	0	-	-	-
1/31/79	2	- am	-7.0	0	2	2	0	0	-	5(1/4")	-	-
2/7/79	3	- am	-	8	-	-	2	2	0	2	-	-
2/14/79	4	- am	-	8	0	0	0	0	-	2	-	-
2/21/79	5	9 am	-	7	BG	BG	3	2	-	3	-	-
2/28/79	6	9 am	-	7	2	2	3	1	0	-	-	Sunny while sampling
3/7/79	7	- am	10	12	B	B	0	0	-	-	3/2/-	-
3/14/79	8	- am	11.5	12	2	2	0	1	-	-	0/0/-	-
3/21/79	9	8 am	18	12	2	2	0	0	-	4	-	Pond II had bubbles
3/28/79	10	- am	11.5	11.5	2	2	2	2	-(SE)	-	2/2/-	-
4/4/79	11	- am	8	12	3	3	0	0	-	3	-	Pond II had bubbles
4/11/79	12	- am	12	12	-	-	-	-	-	-	-	-
4/19/79	13	7 am	-	-	3	3	0	2	-	4	-	Hail Tues, bubbles present
4/25/79	14	8:30 am	12.5	15	3	3	0	0	2	-	0&2/0&2/-	-
5/2/79	15	12:30 pm	20.5	18	3	3	0	0	2	2	0/2/-	-
5/9/79	16	am	10	15	BG	BG	2	2	2	-	-	Clearing today
5/16/79	17	9 am	17	18	2	2	0	0	-	-	0/0/-	Grasses blooming
5/23/79	18	9:30 am	20	19	2	2	0	0	-	2	0/1/-	A lot of grass pollen on Pond I
5/30/79	19	1 pm	29	21	3	3	0	0	-	-	-/-/-	Two truckloads of water removed from Pond II
6/6/79	20	9 am	16	19	3	BG	0	1	-	-	-	-
6/13/79	21	- am	16	19	2	B	0	0	-	2	-	-
6/20/79	22	12 pm	24	21	3	2	0	1	1(SW)	-	-	-
6/27/79	23	12:30 pm	29	23	B	2	0	0	-	2	0/0/2	Pond I smelly with floating detritis
7/4/79	24	9:30 am	20.5	19.5	2	2	0	2	-	-	-	No more grass pollen
7/11/79	25	7:30 am	16	20	3	2	2	2	2(SE)	-	2/2/-	-
7/18/79	26	9 am	23	21.5	2	2	0	0	-	1	0/0/-	-
7/25/79	27	8 am	18.5	20	2	B	0	0	2(SE)	1	0/0/-	-
8/1/79	28	9 am	19	20	3	3	0	0	2(SW)	1	0/0/-	
8/8/79	29	10 am	19.5	19.5	3	3	0	0	2(SW)	1	0/0/-	No rain for a month
8/15/79	30	7:30 am	14	18	3	2	1	2	-	-	0&2/0&1/-	Bubbles in Pond I, many snails in Pond II

Date	Sample Number	Time	Temperature °C Air	Water	Color of Ponds I	II	Weather Notes: Precip	Date of Sampling Cloud Cover	Wind	Temp	Past week ppt/cc/temp	Other Notes
8/22/79	31	7:30 am	15	19	4	3	3	2	-	-	3/2/-	-
8/29/79	32	7:30 am	19	17	4	3	0	2	1(W)	-	0/2/-	-
9/5/79	33	8:30 am	15	19	2	8	3	2	2(SW)	-	2/2/-	Water level high
9/12/79	34	7:45 am	15	19	2	0	0	0	0	-	2/2/-	Water receding, clear the last two days only
9/19/79	35	10:30 am	22	20	4	8	2	0	-	-	0/0/-	High water level
9/26/79	36	9:15 am	18	19	4	0	0	2	2(SW)	-	0/2/-	Low water level
10/3/79	37	9:30 am	18	18	4	8	0	0	2(SW)	2	0/0/2	-
10/10/79	38	11:15 am	21	17	4	3	0	0	2(SW)	2	0/0/2	No rain for a month
10/17/79	39	10:30 am	14	15	8	2	0	0	3(NE)	3	0/2/2	Water turbid, cold at night
10/24/79	40	10 am	13	14	2	2	3	3	3	-	2/2/-	High water level
10/31/79	41	10:15 am	12	13	8	2	0	0	3(NE)	3	2/2/-	-
11/7/79	42	3:30 pm	18	14	2	2	-	-	3	-	-	Turbid water, many grazing protozoa
11/14/79	43	8:30 am	3	8	-	-	0	2	0	3	0/2/-	-
11/21/79	44	9:45 am	2	7	2	1	0	2	0	4	-/-/3	-
11/28/79	45	- am	2	6	0	0	0	0	-	4	-	Ice on puddles
12/5/79	46	- am	4	9	0	0	2	2	-	-	3/2/-	Ponds flooding
12/12/79	47	10 am	5	6	0	0	0	0	1	-	-	Rain last night, water clear
12/19/79	48	9:30 am	10.5	9	0	0	1	1	2(SW)	-	-	Flooding, not turbid
12/26/79												No sample
1/3/80	49	9:30 am	6	8	0	0	3	2	0	-	-	Flooding
1/9/80	50	11:00 am	6	6	0	0	2	2	0	-	2/2/-	Flooding, no odor, began pooling samples
1/16/80	51	- am	9	8	0	0	3	2	0	-	-	Flooding, water turbid
1/23/80	52	1 pm	-	-	0	0	0	0	-	2	0/0/-	Flooding, warming, water clear
1/30/80												Ice on lagoon prevented sampling
2/6/80	53	2 pm	10	7.5	0	2	1	1	-	2	-/-/5 (1")	Ponds flooding, odor at A
2/13/80	54	2 pm	9.5	8	0	2	0	0	2(NE)	2	0/0/2	-

Date	Sample Number	Time	Temperature °C Air	Water	Color of Ponds I	II	Precip	Weather Notes: Date of Sampling Cloud Cover	Wind	Temp	Past week ppt/cc/temp	Other Notes
2/20/80	55	8:30 am	7	8	0	2	0	1	2(SW)	2	2/2/-	Many dipterans swarming, weather changeable
2/27/80	56	1 pm	13.5	12	0	3	2	2	2(SW)	2	2/2/2	Many dipterans, Pond I odor
3/5/80	57	10:30 am	11	12	2	2	2	2	2(SW)	-	0/0/-	Many dipterans
3/12/80	58	2:30 pm	8	9	3	3	3	2	3(SW)	-	3/2/-	Swallows eating dipterans
3/19/80	59	10:00 am	13	10	3	3	1	2	-	-	-	Many dipterans
3/26/80	60	8:30 am	6	11	2	2	2	2	3 -	3	-	-
4/2/80	61	9:30 am	10	12	3	3	-	-	-	-	-	-
4/9/80	62	1:30 pm	15	12	1	2	3	2	3	2	3/2/2	-
4/16/80	63	3:00 pm	25	20	0	3	0	0	0	1	0&2/0&2/-	-
4/23/80	64	11:00 am	19	15.5	0	2	0	0	2(SW)	-	2/2/3	First of grasses blooming
4/30/80	65	9:00 am	10	15	2	3	0	0	1	-	0/0/-	-
5/7/80	66	9:00 am	12	16	2	2	0	0	2(NE)	-	0/1/-	-
5/14/80	67	10:00 am	17	17	2	2	0	0	-	-	0/2/-	-
5/21/80	68	10:00 am	14	17	2	2	0	2	2(SW)	-	0/0/-	-
5/28/80	69	9:30 am	15.5	15.5	3	2	0	2	0	2	-	Humid
6/4/80	70	10:00 am	17	20	2	2	0	1	-	2	0/0/-	-
6/11/80	71	6:45 am	11	17	2	3	0	0	-	3	0/2/-	-
6/18/80	72	3:00 pm	26	26	4	2	0	0	2(NE)	1	-	Humid
6/25/80	73	12:00 pm	12	18	2	2	1	1	2(W)	2	-	Humid (B is greener)
7/2/80	74	8:00 pm	15.5	22	2	2	2	2	3(NW)	-	1/1/-	-
7/9/80	75	10:00 am	15.5	19	2	2	0	2	0	-	0/0&2/-	Hot and clear until 2 days ago, odor in Pond I, end of pollen
7/16/80	76	11:00 am	22	26	4	3	0	0	2(NE)	1	0/2&0/-	Past week cloudy, then clear
7/24/80	77	3:00 pm	28	27	4	2	0	0	2(NE)	1	0/0/1	Very hot week, mill burned Tues, ash on lagoon
7/31/80	78	3:30 pm	28	25	4	3	0	0	2(SW)	1	0/0/1	-
8/7/80	79	3:00 pm	32	27	4	3	0	0	1(SW)	1	0/0/1	Odor from Pond I
8/14/80	80	8:45 pm	15	20	2	2	0	0	3(E)	1	0/0/1	Water mixed by wind

Date	Sample Number	Time	Temperature °C Air	Water	Color of Ponds I	II	Weather Notes Precip	Date of Sampling Cloud Cover	Wind	Temp	Past week ppt/cc/temp	Other Notes
8/21/80	81	4:00 pm	29	25	1	2	0	0	1(NE)	1	0/0/1	Debris floating in Pond I
8/28/80	82	5:30 pm	23	24	1	2	0	0	-	1	0/0/1	-
9/4/80	83	5:30 pm	29	26	2	2	0	0	2(NE)	1	0/0/1	Many dipterans
9/11/80	84	5:15 pm	28	26	3	2	0	1	2(NE)	2	0/1/2/2	No rain for months, fewer dipterans
9/22/80	85	2:00 pm	24.5	19	4	2	0	0	3(NW)	2	2/2/3/3	Odor from Pond I, field burned at lagoon
9/25/80	86	5:00 pm	30	24.5	4	B	0	0	0	1	0/0/1	Sunny since Mon (last sampling)
10/2/80	87	4:30 pm	26	21	4	B	0	0	3(SW)	1	0/0/1	-
10/8/80	88	4:30 pm	22	18	4	B	0	1	3(S)	2	-	Alternately clear and overcast
10/16/80	89	5:00 pm	19	16	3	2	0	1	0	-	0&2/0&2/-	Alternately clear and overcast; rainy weekend
10/23/80	90	1:00 pm	14	14	1	2	0	1	2(SE)	4	0/1/4	-
10/30/80	91	3:30 pm	15.5	12	4	2	0	2	0	3	0&2/1/3	Past week alternately rain and sun
11/6/80	92	2:00 pm	16.5	14	3	1	2	3	3(S)	3	2-0/2/3	Water mixed by wind, rain since yesterday
11/13/80	93	3:00 pm	9	8	2	2	0	2	0	3/4	0/0/4	Past week cold, with hard frosts
11/20/80	94	3:30 pm	14	11	3	4	0	3	0	3	0/3/-	Past week mostly overcast
11/26/80	95	4:30 pm	10	9	3	3	0	1	0	3	-/-/-	-
12/4/80	96	1:45 pm	8	8	0	3	3&4	3	3(SW)	4	3/3/3	Flooding
12/11/80	97	1:00 pm	14	6	0	0	0	0	1(SW)	3	-/-/5(1/2")	1/2" ice on pond M-Th, today ice melting
12/18/80	98	11:30 pm	5	5	2	2	0	3	0	4	-	-
12/25/80	99	3:00 pm	16	11	0	0	3	3	0	3	3/3/-	Raining hard for 2 days, flooding
1/1/81	100	12:00 pm	15	12	0	1	0	0	0	3	0/0/3	Drier and warmer past week
1/8/81	101	3:30 pm	9	8	0	2	0	3	0	4	0/-/4	Past week drier

Appendix B. Abundance of Algae

Mean monthly abundance of phytoplankton species in the sewage lagoon in cells/ml $x(10)^3$. A (+) indicates the presence of an organism at less than 10 cells/ml.

		Actinastrum hantzschii Lagerheim	Agmenellum quadruplicatum Bréb.	Anacystis incerta D.&D.	Ankistrodesmus falcatus (Corda) Ralfs	Chlamydomonas ovata Dang.	Chlamydomonas pertusa Chod.	Chlamydomonas umbonata Pascher
1979	J	0	0	0	0.08	21.84	3.15	0
	F	0	0	0	0.01	2.63	0.98	0.11
	M	0	0	0	0.10	3.24	2.06	2.32
	A	0	0	0	0.04	6.25	3.82	0
	M	0	0	0	0	2.13	1.86	0
	J	0	0	0	1.22	0.69	0.38	151.95
	J	0	0	0	4.77	20.44	0.75	24.84
	A	0	0	0	2.18	51.90	0.12	0
	S	0	1.96	0	0.20	0	0.27	14.75
	O	0.28	142.13	0	0.37	4.97	4.17	1.44
	N	0	0.34	0	0.66	0.15	11.18	0.46
	D	0	0	0	0.16	0	0.56	0.07
1980	J	0	0	0	0.07	0	0	0
	F	0	0	0	0.92	0.13	0	0.07
	M	0	0	0	5.17	35.08	0.13	0
	A	0	0.73	0	0.16	40.99	1.69	0
	M	0	0	0	0.96	410.46	0.58	0
	J	16.38	0	0	5.70	198.26	2.09	0
	J	9.57	4.15	0	2.69	133.94	0.07	193.75
	A	1.57	12.59	0	2.33	0	0	272.47
	S	0	0	0	3.43	23.56	0.18	28.21
	O	0	0	0	0.79	30.16	0.51	0.66
	N	0	0	0	0.40	2.22	0	0.54
	D	0	0	0	0	0.69	0.03	0.03
1981	J	0	0	0	0.03	0.53	0	0

POND I

		Chlorella vulgaris Beijerinck	Chlorogonium elongatum Dang.	Chlorogonium skujae Peterfi	Cryptomonas erosa Ehr.	Cryptomonas sp.	Cyclotella atomus Hust.	Dictyosphaerium ehrenbergianum Naegeli.
1979	J	210.98	0.08	0	0	0	0	0
	F	0	0.15	0	0	0	0	0
	M	0.16	0.22	0	0	0	0	0
	A	24.99	0.17	0	0	0	0	0
	M	3.00	1.46	4.84	0	0	0	0
	J	2.12	2.84	3.55	0.71	0	0	0
	J	0.26	267.04	162.10	7.09	6.49	0	0
	A	0	0.65	54.23	0	0	0	0
	S	0	2.80	1.35	0.12	2.20	0	0
	O	0.08	1.05	3.72	0	0	0	0
	N	0	0.06	0.11	0	0	0	0
	D	0	0	0	0	0	0	0
1980	J	0	0	0	0	0	0	0
	F	0	0	0	0	0	0	0
	M	0	0.56	0.21	0.09	0	0	0
	A	0	0	0	0	0	0	0
	M	212.95	0	0	16.73	0	0	0
	J	100.99	2.16	6.20	1.14	0	0	0
	J	46.16	2.13	14.65	0.61	0	0	2.41
	A	0.39	41.45	9.00	1.01	0	0	7.61
	S	2.70	15.52	10.22	0	0	0	1.65
	O	1.43	0.48	1.85	0.77	0	1.44	5.82
	N	2.14	0	0.22	1.06	0	0.44	0.22
	D	0.71	0.01	0	0.14	0	0.07	0.13
1981	J	1.20	0	0	0	0	0	0.11

POND I

		Euglena pisciformis Klebs.	*Euglena viridis* Ehr.	*Golenkinia radiata* (Chodat.) Willie	*Gomphonema olivaceum* v. *calcarea* cleve	*Kirchneriella obesa* major (Bernard) G.M. Smith	*Mallomonas* sp.	*Navicula* sp.
1979	J	50.38	0	0	0	0	0	0
	F	5.35	12.62	0	0	0	0	0.01
	M	29.34	5.01	0	0	0	0	0
	A	50.77	30.77	0	0	0	0	0
	M	102.76	11.22	0	0	0	0	0
	J	25.21	0	0.06	0	0	0	0
	J	4.26	0	0	0	0	0	0
	A	1.18	1.13	0	0	0	0	0
	S	125.66	41.20	0	0	0	0	0
	O	20.77	52.57	0.02	0	0	0	0
	N	0	24.67	0.03	0	0	0	0
	D	0	0.42	0	0	0	0	0
1980	J	0	0.01	0	0	0	0	0
	F	0	0.65	0	0	0	0	0
	M	0	9.74	0	0	0	0	0
	A	0	0.01	0	0.02	0	0	0
	M	0	0	0	0.19	0	0	0
	J	0	3.70	0.32	0	0	0	0
	J	0	4.83	0	0	0.92	0	0
	A	4.04	7.24	0	0	0	0	0
	S	141.33	60.00	0	0	0	0	0
	O	276.58	7.08	0	0	0.25	0	0
	N	196.59	10.24	0	0	0	0	0
	D	15.26	0.02	0	0	0	0.01	0
1981	J	12.55	0	0	0	0	0	0

POND I

		Nitzschia sp.	Nostoc commune Vauch.	Oscillatoria lutea Agardh	Phacus turgidulus Pochmann	Pteromonas angulosa Lemm.	Pteromonas sp.	Scenedesmus acuminatus (Lag.) Chodat.
1979	J	0	0	0	0	0	0	0.16
	F	0	0	0	0	0.32	0	0
	M	0	0	0.04	0	0	0	0
	A	0	0	0	0	0	0.68	0
	M	0	0	0	0	0	2.20	0.06
	J	0	0	0.03	0	4.06	9.19	0.43
	J	0	0	0.26	0	4.72	1.91	10.42
	A	0	0	0.26	0	2.43	57.50	16.08
	S	0	0	0.27	0	0.24	0.48	1.01
	O	0.04	0	0.19	0	0.24	0.26	1.74
	N	0	0	0.12	0	0.34	0.20	0.12
	D	0.01	0	0.06	0	0.01	0.02	0.09
1980	J	0	0	0	0	0	0	0.03
	F	0	0	0	0	0	0	0.05
	M	0	0	0	0	0	0.21	1.38
	A	0.18	0	0	0	0	0	0.04
	M	0.19	0	0	0	0	0	10.58
	J	0	0	0	0	0	2.16	12.00
	J	0	0	6.92	0	0	21.79	26.08
	A	0.52	0.48	8.01	1.54	0.69	0.77	37.02
	S	0	0	3.25	3.20	1.34	0	19.00
	O	0	0.63	1.58	1.02	0.46	0	11.75
	N	0	0	0.54	0.10	0	0	1.74
	D	0	0	0	0.01	0	0	0.49
1981	J	0	0	0	0.30	0	0	0.21

POND I

		Scenedesmus armatus (Chod.) Smith	Scenedesmus obliquus (Turp.)	Schizothrix calcicola (Agardh) Gomont	Sphaerocystis schroeteri Chodat.	Sticchococcus chodati (Bail.) Heering	Tetraëdron minimum (A. Braun) Hansgirg	Trachelomonas hispida (Perty) Stein emend. Deflandre
1979	J	0	0	57.13	0	2.02	0	1.04
	F	0.19	0	50.80	0	0	0	2.60
	M	0.11	0	17.18	0	0	0	3.65
	A	0	0	11.16	0	0	0	0.29
	M	0	0	0	0	0	0	0.11
	J	0.47	0	0.05	0	0	0	0
	J	3.98	0	2.71	0	0	0	0
	A	6.17	0	0	0	0	0	0
	S	0	0	0	0	0	0	0
	O	0.43	1.24	0.66	0	0	0	0
	N	0.03	2.25	0.09	0	0	0	0
	D	0.05	0.63	0.24	0	0	0.01	0
1980	J	0.04	0.01	0.04	0	0	0	0
	F	0.08	0	0.45	0	0	0	0
	M	0.40	0	3.38	0	0	0	0.07
	A	0.05	0.03	5.39	0	0	0	0
	M	0.91	0	23.28	0	0	0	0
	J	1.23	0.19	3.74	0	0	0	1.53
	J	0.60	2.31	7.11	0	0	0	5.98
	A	2.33	5.50	5.59	0	0	0.48	0.74
	S	3.00	1.25	4.05	0	0	0	0.66
	O	0.88	2.36	0	0	0	0.43	1.78
	N	0.91	0.82	6.76	0	1.77	0	3.72
	D	0.36	0.26	4.38	0	0	0	0.11
1981	J	0.97	0.18	1.99	0	0	0.03	0.06

POND I

		Actinastrum hantzschii Lagerheim	Agmenellum quadruplicatum Bréb.	Anacystis incerta D&D	Ankistrodesmus falcatus (Corda) Ralfs	Chlamydomonas ovata Dang.	Chlamydomonas pertusa Chod.	Chlamydomonas umbonata Pascher
1979	J	0	0	0	1.00	12.41	4.25	0
	F	0	0	0	0.18	5.43	2.42	0.84
	M	0	0	2.86	0.68	73.73	2.86	4.46
	A	0	0	0.06	0.40	10.11	10.59	0
	M	0	0	0	0.46	3.10	0.69	0.15
	J	14.14	1.96	2.00	4.05	19.79	0.72	49.96
	J	0	9.23	0	3.70	21.25	0.73	3.59
	A	0	0	0	1.54	16.50	0	0
	S	0	0	0	0	24.99	0	1.92
	O	0.13	0.43	0	0.97	4.80	3.81	3.84
	N	0	0	0	1.28	0	36.93	1.73
	D	0	0	0	0.59	0	1.05	0.10
1980	J	0	0	0	0.25	+	0.02	0.03
	F	0	0	0	0.91	28.43	0.95	9.73
	M	0.28	0	0	2.27	34.97	5.44	0.08
	A	0	0	0	0.03	32.18	6.92	0
	M	0	0	0	0.99	92.68	3.52	0
	J	7.43	1.09	0	2.97	39.59	0.94	0
	J	0.85	10.46	0	8.65	48.90	0.72	4.73
	A	0	0	46.17	0.96	48.33	0	28.37
	S	0	0	5.77	1.84	0.99	0	15.39
	O	0	0	0	1.36	28.02	0	0
	N	0	0	0	0.38	25.23	0.14	2.75
	D	0	0	0	0.07	1.19	0.02	0
1981	J	0	0	0	0.10	1.98	0.06	0

POND II

		Chlorella vulgaris Beijerinck	*Chlorogonium elongatum* Dang.	*Chlorogonium skujae* Peterfi	*Cryptomonas erosa* Ehr.	*Cryptomonas* sp.	*Cyclotella atomus* Hust.	*Dictyosphaerium ehrenbergianum* Naegeli.
1979	J	0	0	0	0	0	0	0
	F	0	0	0	0	0	0	0
	M	0	1.08	0	0	0	0	0
	A	971.08	0.74	0	0	0	0	0
	M	22.12	0.85	2.05	0.76	0	0	0
	J	31.34	1.02	21.12	0.12	0	0	0
	J	24.75	2.71	9.02	0.79	0	0	0
	A	0	0.11	2.07	0.45	0	0	6.51
	S	0.06	0	0.01	5.56	0	0	0
	O	0	0.31	1.82	2.04	0	0	0
	N	0	0.18	0.54	0.37	0	0	0
	D	0	0.02	0	0.02	0	0	0
1980	J	0	0	0	0	0	0	0
	F	0	0	0	0	0	0	0
	M	0	0.18	0.28	0.37	0	0	0
	A	5.51	0.45	0.22	0.27	0	1.65	0.72
	M	20.47	0.62	0.41	0.78	0	0	0
	J	10.99	1.41	1.81	0.25	0	0	0
	J	62.85	3.23	2.22	1.78	0	5.77	86.20
	A	0	0	1.44	2.88	0	40.40	8.18
	S	0.26	0	0	0.72	0	110.46	7.21
	O	2.31	0.40	0	0.45	0	51.09	1.89
	N	0.52	0	0.89	1.51	0	15.23	7.78
	D	1.81	0	0	0.11	0	0.31	1.65
1981	J	1.37	0.04	0	0.04	0	0.13	1.32

POND II

		Euglena pisciformis Klebs.	*Euglena viridis* Ehr.	*Golenkinia radiata* (Chodat.) Willie	*Gomphonema olivaceum* v. *calcarea* Cleve	*Kirchneriella obesa major* (Bernard) G.M. Smith	*Mallomonas* sp.	*Navicula* sp.
1979	J	33.36	0	0	0	0	0	0
	F	17.05	11.44	0.04	0	0	0	0.07
	M	9.05	0.40	0	0	0.02	0	0
	A	37.38	9.83	0	0	0.46	0	0
	M	106.98	7.50	0	0	0.12	0	0
	J	7.84	1.42	0	0	29.59	0	0
	J	0.61	2.64	0	0	1.54	0	0
	A	0.09	0.40	0	0	0	0	0
	S	0.55	0.39	0	0.08	0	0	0.10
	O	1.31	9.78	0	0	2.35	0	0.12
	N	0.74	30.34	0.02	0	1.17	0	0
	D	0.04	1.26	0.37	0	0	0	0
1980	J	0	0.08	0	0	+	0	0.02
	F	0	1.04	0	0	0	0	0
	M	0	13.60	0	0	0	0	0
	A	0	0.10	0	0	0	0	0
	M	0	0.80	0	0	0	0	0
	J	0.18	2.13	0.22	0	22.61	0	0
	J	0.72	0.42	0	0	13.71	0	0
	A	0.72	0	0	0	2.16	0	0
	S	0	0.24	4.33	0	0	0	0
	O	4.18	0.52	0	0	11.37	0	0
	N	88.26	1.19	0	0	0.62	0	0
	D	78.61	0.05	0	0	0	0	0
1981	J	7.75	0	0	0	0	0	0

POND II

		Nitzschia sp	*Nostoc commune* Vauch.	*Oscillatoria lutea* Agardh	*Phacus turgidulus* Pochmann	*Pteromonas angulosa* Lemm.	*Pteromonas* sp.	*Scenedesmus acuminatus* (Lag.) Chodat.
1979	J	0.48	0	0.06	0	0.06	0	1.21
	F	0	0	0.03	0	0.52	0	0.58
	M	0	0	0	0	0.04	0.03	1.64
	A	0	0	0	0	0.15	3.06	1.07
	M	1.29	0	0	0	0.77	4.33	0.48
	J	0.18	0	1.97	0	4.89	15.66	16.10
	J	0	0	34.38	0	0	60.19	84.76
	A	0	0	43.51	0	0	6.35	149.05
	S	0.08	0	0.19	0	0	0	2.03
	O	0.19	0	0.18	0	0	0.20	2.87
	N	0	0	0.62	0	0.29	0.93	3.94
	D	0	0	0.85	0	0.03	0.04	0.19
1980	J	0	0	0	0	0	0	0.08
	F	0.84	0	0.21	0	0	0	0.05
	M	0	0	0.07	0	0	0.35	1.65
	A	0	0	0.03	0	0	1.79	0.83
	M	0	0	0.43	0	0	0.05	0.74
	J	0	0	42.09	0	0	0	6.39
	J	0	0	0.46	0	0	0.26	112.61
	A	0.72	185.87	2.16	0.48	0	0	201.67
	S	0	4.57	3.31	0	0	0	38.40
	O	0	0.82	1.31	0	0.12	0	16.99
	N	0	0	0.62	0	0.24	0	8.87
	D	0.02	2.47	0.05	0.02	0	0	1.47
1981	J	0	0	0	0	0	0	0.72

POND II

		Scenedesmus armatus (Chod.) Smith	Scenedesmus obliquus (Turp.) Kutz.	Schizothrix calcicola (Agardh) Gomont	Sphaerocystis schroeteri Chodat.	Sticchococcus chodati (Bail.) Heering	Tetraëdron minimum (A. Braun) Hansgirg	Trachelomonas hispida (Perty) Stein emend. Deflandre
1979	J	0.94	0.41	16.98	0	0	0	3.04
	F	0.19	0.20	34.29	0	0	0	2.02
	M	1.15	0.17	4.82	0	0	0	6.17
	A	1.33	0.22	6.63	0	0	0	1.10
	M	1.46	0.07	0.24	0	0	0	0.48
	J	7.47	1.16	0.92	0	0	0	2.66
	J	4.23	27.59	1.04	0	0	0	1.98
	A	6.53	163.94	0	0	0	0.35	3.44
	S	0	25.32	0	0	0	0.03	0.05
	O	1.27	185.43	1.02	0	0	0.84	0.22
	N	0.97	102.58	0.31	0	0	1.49	0.15
	D	0.64	8.14	0.13	0	0	0.05	0.12
1980	J	0.24	0.42	+	0.03	0	+	0
	F	0.42	0.14	0.11	0	0	0	0
	M	1.02	1.48	1.09	0	0	0.14	0
	A	1.55	0.59	3.33	0	0	0	0.06
	M	1.13	0.63	4.03	0	0	0.15	0.13
	J	5.94	6.01	0.42	0	0	0.22	0
	J	34.12	202.12	15.08	0	0	27.00	2.18
	A	83.44	183.31	2.40	0	0	21.40	0
	S	244.43	4.19	0.26	0	0	3.41	0.26
	O	234.28	24.99	0.60	0	0	17.70	0.64
	N	52.80	35.16	0.38	0	0.24	5.96	0.93
	D	8.35	0.94	1.69	0	0	0.10	0.12
1981	J	5.02	0.08	2.22	0	0	0.26	0.12

POND II

Appendix C. Abundance of Parasites

The weekly abundance of each host, zoospores of parasites, and dead host cells are reported. Fractions of infected and dead host cells are also included. Brackets [ ] indicate values computed by an alternate method (see methods). Missing data is indicated by a (-) dash. The total number of cells of species of algae parasitized by *Aphelidium chlorococcarum* compared to the total number of zoospores of this parasite is listed in the last table.

Scenedesmus obliquus

Year	Month	Week	Host Cells/ml	Fraction of Zoospores	Fraction of Dead Hosts	Zoospores Cells/ml	Dead Hosts Cells/ml
1979	J	1	683	0	0	0	0
		2	145	0	0	0	0
	F	3	137	0	0	0	0
		4	464	0	0	0	0
		5	42	0	0.125	0	5
		6	166	0	0	0	0
	M	7	285	0	0.024	0	6
		8	0	0	0	0	0
		9	0	-	-	-	-
		10	241	0	0	0	0
	A	11	514	0	0.057	0	29
		12	100	0	0	0	0
		13	246	0	0	0	0
		14	3	0	0	0	0
	M	15	0	0	0	0	0
		16	0	0	0	0	0
		17	0	-	-	-	-
		18	48	0	0	0	0
		19	304	0	0	0	0
	J	20	823	0.259	0.200	213	164
		21	2021	0	0.087	0	175
		22	577	0	0	0	0
		23	1205	-	-	-	-
	J	24	3179	0	0	0	0
		25	10402	0.075	0	780	0
		26	31293	0	0	0	0
		27	65500	0.009	0	589	0
	A	28	67675	0.007	0.013	473	879
		29	240065	0	0.067	0	16084
		30	243989	0	0.015	0	3659
		31	163962	0	0	0	0
		32	104015	0	0	0	0
	S	33	26675	0	0.011	0	293
		34	249	0.026	0	6	0
		35	30020	0	0	0	0
		36	44323	0.007	0	310	0
	O	37	86469	-	-	-	-
		38	362985	0.003	0.003	1088	1088
		39	215579	-	-	-	-
		40	192747	0.008	0.041	1541	7902
		41	69394	0.091	0.095	6314	6592
	N	42	177185	0.009	0.015	1594	2657
		43	51543	0.006	0.016	309	824
		44	158189	0.007	0.007	1107	1170
		45	23393	0	0.011	0	257
	D	46	10951	0.131	0	1434	0
		47	10038	-	-	-	-
		48	3439	0	0.132	0	453

Scenedesmus obliquus

Year	Month	Week	Host Cells/ml	Fraction of Zoospores	Fraction of Dead Hosts	Zoospores Cells/ml	Dead Hosts Cells/ml
1980	J	49	482	0.014	0	6	0
		50	344	-	-	-	-
		51	417	0.046	0.074	19	30
		52	417	0.064	0.326	26	136
	F	53	315	0.018	0.188	5	59
		54	228	-	-	-	-
		55	0	-	-	-	-
		56	0	0.222	0	0	0
	M	57	1562	0	0.187	0	292
		58	1136	0	0.296	0	336
		59	83	-	-	-	-
		60	3144	0	0.209	0	657
	A	61	926	-	-	-	-
		62	827	0	0.067	0	55
		63	0	0	0	0	0
		64	0	0	0	0	0
		65	1183	-	-	-	-
	M	66	0	0	0	0	0
		67	0	0	0	0	0
		68	2528	-	-	-	-
		69	0	0	0.154	0	0
	J	70	1256	0	0	0	0
		71	3572	0	0	0	0
		72	7620	-	-	-	-
		73	11599	0.111	0.036	1287	417
	J	74	7722	0	0.020	0	154
		75	62273	0	0.008	0	498
		76	130412	0	0	0	0
		77	1892	0.253	0.188	478	355
		78	808286	0	0	0	0
	A	79	236075	-	-	-	-
		80	407177	0	0.026	0	1044
		81	77239	0.018	0.017	1390	1313
		82	12738	0.077	0.037	980	471
	S	83	3509	0	0	0	0
		84	3911	0	0	0	0
		85	8107	0	0	0	0
		86	1240	0	0	0	0
	O	87	10613	0	0	0	0
		88	18162	0	0	0	0
		89	12437	0	0	0	0
		90	38322	0	0.022	0	843
		91	45401	0	0	0	0
	N	92	53368	0	0	0	0
		93	43674	0	0	0	0
		94	33628	0.009	0	302	0
		95	9971	0	0	0	0
	D	96	324	0	0	0	0
		97	557	0	0.333	0	185
		98	1870	0	0	0	0
		99	992	0	0	0	0
1981	J	100	171	0	0.026	0	4
		101	0	1.000	0	0	0

Scenedesmus armatus

Year	Month	Week	Host Cells/ml	Fraction of Zoospores	Fraction of Dead Hosts	Zoospores Cells/ml	Dead Hosts Cells/ml
1979	J	1	0	0	0	0	0
		2	1877	0	0	0	0
	F	3	0	0	0	0	0
		4	0	0	0	0	0
		5	0	0	0	0	0
		6	755	0	0	0	0
	M	7	81	0	0	0	0
		8	635	0	0	0	0
		9	1371	-	-	-	-
		10	2534	0	0	0	0
	A	11	2053	0.008	0.008	16	16
		12	608	0	0	0	0
		13	2673	0	0.360	0	962
		14	[10]	0.330	0	0	0
	M	15	[1419]	0.027	0.075	0	0
		16	[77]	0.200	0.583	0	0
		17	2151	-	-	-	-
		18	4191	0	0	0	0
		19	953	0.048	0.095	45	90
	J	20	11492	0.166	0.309	1907	3551
		21	3667	0.015	0.164	55	601
		22	9780	0.020	0	195	0
		23	4955	-	-	-	-
	J	24	9520	0.740	0.643	7044	612
		25	3956	0.649	0.233	2567	921
		26	3443	0	0.400	0	1377
		27	0	0	0.385	0	0
	A	28	1139	0	0	0	0
		29	13011	0	0	0	0
		30	16058	0	0	0	0
		31	2442	0	0	0	0
		32	0	0	0	0	0
	S	33	0	0	0	0	0
		34	0	0	0	0	0
		35	0	0	0	0	0
		36	0	0	0	0	0
	O	37	4001	-	-	-	-
		38	[6868]	0	0.750	0	[5151]
		39	0	-	-	-	-
		40	2347	0	0	0	0
		41	0	0	0	0	0
	N	42	1746	0	0	0	0
		43	0	0	0	0	0
		44	1467	0	0.400	0	586
		45	652	0.167	0.143	108	93
	D	46	814	0	0	0	0
		47	651	-	-	-	-
		48	458	0	0	0	0

Scenedesmus armatus

Year	Month	Week	Host Cells/ml	Fraction of Zoospores	Fraction of Dead Hosts	Zoospores Cells/ml	Dead Hosts Cells/ml
1980	J	49	139	0	0.273	0	38
		50	190	-	-	-	-
		51	200	0.048	0.208	9	41
		52	453	0.037	0.143	16	64
	F	53	307	0	0.219	0	67
		54	1367	-	-	-	-
		55	0	-	-	-	-
		56	0	0	0	0	0
	M	57	1071	0	0.059	0	63
		58	1045	0	0	0	0
		59	0	-	-	-	-
		60	1958	0	0.074	0	144
	A	61	1214	-	-	-	-
		62	4702	0.043	0.021	202	98
		63	0	0	0	0	0
		64	1025	0.100	0	102	0
		65	789	-	-	-	-
	M	66	3957	0	0	0	0
		67	577	0	0	0	0
		68	0	-	-	-	-
		69	0	0	0	0	0
	J	70	1615	0.100	0.167	161	269
		71	1598	0.046	0	73	0
		72	16294	-	-	-	-
		73	4261	0.222	0.100	946	426
	J	74	7694	0	0	0	0
		75	29019	0.016	0	464	0
		76	76177	0	0	0	0
		77	[674]	0.559	0.227	[377]	[153]
		78	57710	0.100	0.048	5771	2770
	A	79	84641	-	-	-	-
		80	176015	0.324	0.146	57029	25698
		81	46168	0.535	0.368	24699	16989
		82	26931	0.068	0.048	1831	1292
	S	83	105801	0.072	0.060	7617	6348
		84	321733	0.003	0.016	965	5147
		85	334718	0.024	0.019	8033	6359
		86	215450	0.010	0.020	2154	4309
	O	87	403970	0	0	0	0
		88	410895	0.021	0.010	8628	4108
		89	209198	0.061	0.078	12761	16317
		90	64058	0.424	0.300	27160	19217
		91	83267	0.194	0.202	16153	16819
	N	92	55786	0.246	0.218	13723	12161
		93	43859	0.066	0.046	2894	2017
		94	62656	0.031	0.036	1942	2255
		95	48916	0.020	0.033	978	1614
	D	96	0	0	0.043	0	0
		97	8280	0.006	0.029	49	240
		98	18466	0	0.087	0	1606
		99	6668	0.006	0.006	40	40
	J	100	8464	0.036	0.013	304	110
1981		101	1577	0	0	0	0

Scenedesmus acuminatus

Year	Month	Week	Host Cells/ml	Fraction of Zoospores	Fraction of Dead Hosts	Zoospores Cells/ml	Dead Hosts Cells/ml
1979	J	1	1492	0	0	0	0
		2	919	0.008	0.016	8	15
	F	3	645	0	0	0	0
		4	1248	0	0	0	0
		5	93	0	0	0	0
		6	333	0	0	0	0
	M	7	295	0	0	0	0
		8	0	0	0	0	0
		9	0	-	-	-	-
		10	2626	0	0.007	0	18
	A	11	1679	0	0.043	0	72
		12	338	0	0	0	0
		13	2100	0.023	0.022	48	46
		14	159	0	0	0	0
	M	15	0	0	0	0	0
		16	0	0	0	0	0
		17	0	-	-	-	-
		18	999	0	0	0	0
		19	1409	0.050	0.056	70	79
	J	20	13542	0.007	0.073	95	988
		21	17418	0.055	0.103	958	1794
		22	17517	0.008	0.042	140	736
		23	15943	-	-	-	-
	J	24	26163	0	0.026	0	680
		25	36542	0.022	0.078	804	2850
		26	50448	0	0.020	0	1009
		27	225870	0.003	0.003	678	678
	A	28	122996	0	0.007	0	861
		29	293721	0	0.076	0	22323
		30	187178	0	0.032	0	5990
		31	116253	0	0.007	0	814
		32	25089	0	0.014	0	351
	S	33	3030	0.032	0.114	97	345
		34	395	0.033	0.017	13	7
		35	2582	0	0	0	0
		36	2117	0	0.125	0	265
	O	37	2303	-	-	-	-
		38	2352	1.000	0	2352	0
		39	3047	-	-	-	-
		40	4215	0	0	0	0
		41	2413	0	0	0	0
	N	42	10398	0	0.100	0	1040
		43	854	0	0	0	0
		44	2705	0	0	0	0
		45	1807	0	0.045	0	81
	D	46	352	0.005	0	2	0
		47	194	-	-	-	-
		48	23	0	0.670	0	15

Scenedesmus acuminatus

Year	Month	Week	Host Cells/ml	Fraction of Zoospores	Fraction of Dead Hosts	Zoospores Cells/ml	Dead Hosts Cells/ml
1980	J	49	75	0	0.143	0	11
		50	46	-	-	-	-
		51	46	0	0.444	0	21
		52	154	0.232	0.381	36	59
	F	53	94	0	0.407	0	38
		54	113	-	-	-	-
		55	0	-	-	-	-
		56	0	0	0	0	0
	M	57	1347	0	0.083	0	112
		58	1302	0	0.119	0	155
		59	97	-	-	-	-
		60	3850	0	0.023	0	88
	A	61	1199	-	-	-	-
		62	1310	0	0.240	0	314
		63	456	0	0	0	0
		64	0	0	0	0	0
		65	1183	-	-	-	-
	M	66	1978	0	0	0	0
		67	432	0	0	0	0
		68	549	-	-	-	-
		69	0	0	0	0	0
	J	70	4052	0.012	0.024	49	97
		71	2465	0	0.210	0	518
		72	6501	-	-	-	-
		73	12549	0.069	0.064	866	803
	J	74	18054	0.008	0.061	144	1101
		75	51168	0.042	0.040	2149	2047
		76	77343	0.012	0.069	928	5337
		77	1302	0.016	0.135	21	176
		78	415165	0.012	0	4982	0
	A	79	144810	-	-	-	-
		80	317083	0.023	0.022	7293	6976
		81	280563	0.014	0.028	3928	7856
		82	64207	0.008	0.023	514	1477
	S	83	67666	0	0.063	0	4263
		84	50913	0	0.206	0	10488
		85	34213	0	0.107	0	3660
		86	811	0	0.059	0	48
	O	87	6699	0	0.143	0	958
		88	15694	0	0	0	0
		89	13532	0	0.040	0	541
		90	13616	0.062	0	844	0
		91	35391	0.043	0	1522	0
	N	92	19730	0	0	0	0
		93	7687	0.029	0.028	223	215
		94	2646	0	0	0	0
		95	5418	0	0.017	0	92
	D	96	115	0	0.091	0	10
		97	1274	0	0.061	0	78
		98	3259	0	0.033	0	107
		99	1230	0	0	0	0
1981	J	100	1282	0	0	0	0
		101	153	0	0.889	0	137

Actinastrum hantzschii

Year	Month	Week	Host Cells/ml	Fraction of Zoospores	Fraction of Dead Hosts	Zoospores Cells/ml	Dead Hosts Cells/ml
1979	J	1	0	0	0	0	0
		2	0	0	0	0	0
	F	3	0	0	0	0	0
		4	0	0	0	0	0
		5	0	0	0	0	0
		6	0	0	0	0	0
	M	7	0	0	0	0	0
		8	0	0	0	0	0
		9	0	-	-	-	-
		10	0	0	0	0	0
	A	11	0	0	0	0	0
		12	0	0	0	0	0
		13	0	0	0	0	0
		14	0	0	0	0	0
	M	15	0	0	0	0	0
		16	0	0	0	0	0
		17	0	-	-	-	-
		18	0	0	0	0	0
		19	0	0	0	0	0
	J	20	14060	0	0	0	0
		21	22373	0	0.875	0	19577
		22	17116	0	0	0	0
		23	2999	-	-	-	-
	J	24	0	0	0	0	0
		25	0	0	0	0	0
		26	0	0	0	0	0
		27	0	0	0	0	0
	A	28	0	0	0	0	0
		29	0	0	0	0	0
		30	0	0	0	0	0
		31	0	0	0	0	0
		32	0	0	0	0	0
	S	33	0	0	0	0	0
		34	0	0	0	0	0
		35	0	0	0	0	0
		36	0	0	0	0	0
	O	37	0	-	-	-	-
		38	0	0	0	0	0
		39	0	-	-	-	-
		40	0	0	0	0	0
		41	652	0	0	0	0
	N	42	0	0	0	0	0
		43	0	0	0	0	0
		44	0	0	0	0	0
		45	0	0	0	0	0
	D	46	0	0	0	0	0
		47	0	-	-	-	-
		48	0	0	0	0	0

Actinastrum hantzschii

Year	Month	Week	Host Cells/ml	Fraction of Zoospores	Fraction of Dead Hosts	Zoospores Cells/ml	Dead Hosts Cells/ml
1980	J	49	0	0	0	0	0
		50	0	-	-	-	-
		51	0	0	0	0	0
		52	0	0	0	0	0
	F	53	0	0	0	0	0
		54	0	-	-	-	-
		55	0	-	-	-	-
		56	0	0	0	0	0
	M	57	0	0	0	0	0
		58	0	0	0	0	0
		59	0	-	-	-	-
		60	1119	0	0	0	0
	A	61	0	-	-	-	-
		62	0	0	0	0	0
		63	0	0	0	0	0
		64	0	0	0	0	0
		65	0	-	-	-	-
	M	66	0	0	0	0	0
		67	0	0	0	0	0
		68	0	-	-	-	-
		69	0	0	0	0	0
	J	70	0	0	0	0	0
		71	1420	0	0	0	0
		72	2715	-	-	-	-
		73	25569	0	0	0	0
	J	74	4232	0.250	0.742	1058	3140
		75	0	0	0.200	0	0
		76	0	0	0	0	0
		77	0	0	0	0	0
		78	0	0	0	0	0
	A	79	0	-	-	-	-
		80	0	0	0	0	0
		81	0	0	0	0	0
		82	0	0	0	0	0
	S	83	0	0	0	0	0
		84	0	0	0	0	0
		85	0	0	0	0	0
		86	0	0	0	0	0
	O	87	0	0	0	0	0
		88	0	0	0	0	0
		89	0	0	0	0	0
		90	0	0	0	0	0
		91	0	0	0	0	0
	N	92	0	0	0	0	0
		93	0	0	0	0	0
		94	0	0	0	0	0
		95	0	0	0	0	0
	D	96	0	0	0	0	0
		97	0	0	0	0	0
		98	0	0	0	0	0
		99	0	0	0	0	0
1981	J	100	0	0	0	0	0
		101	0	0	0	0	0

Ankistrodesmus falcatus

Year	Month	Week	Host Cells/ml	Fraction of Zoospores	Fraction of Dead Hosts	Zoospores Cells/ml	Dead Hosts Cells/ml
1979	J	1	1790	0	0	0	0
		2	209	0	0	0	0
	F	3	209	0	0	0	0
		4	182	0	0.200	0	36
		5	135	0	0	0	0
		6	205	0	0	0	0
	M	7	494	0	0	0	0
		8	495	0	0	0	0
		9	266	-	-	-	-
		10	1467	0	0	0	0
	A	11	1201	0.021	0.040	25	48
		12	112	0	0	0	0
		13	195	0	0	0	0
		14	112	0	0	0	0
	M	15	0	0	0	0	0
		16	0	0	0	0	0
		17	293	0	0	0	0
		18	1047	0	0	0	0
		19	978	0	0	0	0
	J	20	6235	0	0.015	0	93
		21	4034	0.034	0.037	137	149
		22	2322	0	0	0	0
		23	3618	-	-	-	-
	J	24	2543	0.070	0	178	0
		25	6628	0	0	0	0
		26	2564	0	0	0	0
		27	3077	0	0	0	0
	A	28	0	0	0	0	0
		29	2608	0	0	0	0
		30	5107	0	0	0	0
		31	0	0	0	0	0
		32	0	0	0	0	0
	S	33	0	0	0	0	0
		34	0	0	0	0	0
		35	0	0	0	0	0
		36	0	0	0	0	0
	O	37	0	0	0	0	0
		38	733	0	0	0	0
		39	2029	0	0	0	0
		40	1760	0	0	0	0
		41	326	0	0	0	0
	N	42	3772	0	0	0	0
		43	1105	0	0	0	0
		44	0	0	0	0	0
		45	254	0	0	0	0
	D	46	900	0	0	0	0
		47	562	-	-	-	-
		48	297	0	0.250	0	74

Ankistrodesmus falcatus

Year	Month	Week	Host Cells/ml	Fraction of Zoospores	Fraction of Dead Hosts	Zoospores Cells/ml	Dead Hosts Cells/ml
1980	J	49	139	0	0.091	0	12
		50	70	-	-	-	-
		51	216	0.016	0	3	0
		52	591	0.040	0	23	0
	F	53	410	0.022	0	9	0
		54	1709	-	-	-	-
		55	0	-	-	-	-
		56	1519	0	0	0	0
	M	57	5053	0.105	0.050	503	252
		58	2090	0.074	0	154	0
		59	0	-	-	-	-
		60	1958	0.053	0	103	0
	A	61	151	-	-	-	-
		62	0	0	0	0	0
		63	0	0	0	0	0
		64	0	0	0.500	0	0
		65	0	-	-	-	-
	M	66	3297	0	0	0	0
		67	72	0	0	0	0
		68	0	-	-	-	-
		69	577	0	0	0	0
	J	70	923	0	0	0	0
		71	710	0	0	0	0
		72	5974	-	-	-	-
		73	4261	0	0	0	0
	J	74	18851	0.143	0.204	2695	3845
		75	10552	1.000	0.222	10552	2342
		76	2308	0.600	0.375	1385	865
		77	0	0.330	0.250	0	0
		78	11542	0	0	0	0
	A	79	3847	-	-	-	-
		80	0	0	0	0	0
		81	0	0.500	0	0	0
		82	0	0	0.167	0	0
	S	83	3847	0	0	0	0
		84	1442	0	0	0	0
		85	0	0	0	0	0
		86	2051	0	0	0	0
	O	87	1442	0	0	0	0
		88	0	0	0	0	0
		89	2885	0	0	0	0
		90	0	0	0	0	0
		91	2473	0.330	0	816	0
	N	92	961	0.500	0.330	480	317
		93	577	0	0	0	0
		94	0	0	0	0	0
		95	0	0	0	0	0
	D	96	0	0	0	0	0
		97	73	0	0	0	0
		98	205	0	0	0	0
		99	0	0	0	0	0
1981	J	100	170	0	0	0	0
		101	38	0	0	0	0

Tetraëdron minimum

Year	Month	Week	Host Cells/ml	Fraction of Zoospores	Fraction of Dead Hosts	Zoospores Cells/ml	Dead Hosts Cells/ml
1979	J	1	0	0	0	0	0
		2	0	0	0	0	0
	F	3	0	0	0	0	0
		4	0	0	0	0	0
		5	0	0	0	0	0
		6	0	0	0	0	0
	M	7	0	0	0	0	0
		8	0	0	0	0	0
		9	0	-	-	-	-
		10	0	0	0	0	0
	A	11	0	0	0	0	0
		12	0	0	0	0	0
		13	0	0	0	0	0
		14	0	0	0	0	0
	M	15	0	0	0	0	0
		16	0	0	0	0	0
		17	0	-	-	-	-
		18	0	0	0	0	0
		19	0	0	0	0	0
	J	20	0	0	0	0	0
		21	0	0	0	0	0
		22	0	0	0	0	0
		23	0	-	-	-	-
	J	24	0	0	0	0	0
		25	0	0	0	0	0
		26	0	0	0	0	0
		27	0	0	0	0	0
	A	28	0	0	0	0	0
		29	0	0	0	0	0
		30	0	0	0	0	0
		31	699	0	0	0	0
		32	1049	0	0.20	0	209
	S	33	122	0	0	0	0
		34	0	0	0	0	0
		35	0	0	0	0	0
		36	0	0	0	0	0
	O	37	0	-	-	-	-
		38	733	0	0	0	0
		39	1344	-	-	-	-
		40	2127	0	0	0	0
		41	0	0	0	0	0
	N	42	5169	0	0	0	0
		43	209	0	0	0	0
		44	0	0	0	0	0
		45	572	0	0	0	0
	D	46	62	0	0	0	0
		47	92	-	-	-	-
		48	0	0	0	0	0

Tetraëdron minimum

Year	Month	Week	Host Cells/ml	Fraction of Zoospores	Fraction of Dead Hosts	Zoospores Cells/ml	Dead Hosts Cells/ml
1980	J	49	0	0	0	0	0
		50	0	-	-	-	-
		51	8	0	0	0	0
		52	0	0	0	0	0
	F	53	0	0	0.500	0	0
		54	0	-	-	-	-
		55	0	-	-	-	-
		56	0	0	0	0	0
	M	57	0	0	1.000	0	0
		58	0	0	0	0	0
		59	0	-	-	-	-
		60	559	0	0	0	0
	A	61	0	-	-	-	-
		62	0	0	0	0	0
		63	0	0	0	0	0
		64	0	0	0	0	0
		65	0	-	-	-	-
	M	66	0	0	0	0	0
		67	72	0	0	0	0
		68	512	-	-	-	-
		69	0	0	0	0	0
	J	70	0	0	0	0	0
		71	355	0	0	0	0
		72	543	-	-	-	-
		73	0	0	0	0	0
	J	74	1923	0	0	0	0
		75	2638	0	0	0	0
		76	9233	0	0	0	0
		77	0	0	0	0	0
		78	121191	0	0	0	0
	A	79	75023	-	-	-	-
		80	5771	0	0.500	0	2885
		81	2885	0	0.500	0	1442
		82	1923	0	0	0	0
	S	83	0	0	0	0	0
		84	2885	0	0	0	0
		85	7694	0	0	0	0
		86	3077	0	0	0	0
	O	87	12984	0	0	0	0
		88	23084	0.028	0	646	0
		89	23084	0.053	0.017	1223	392
		90	16158	0.219	0.146	3538	2359
		91	13190	0.461	0.350	6080	4616
	N	92	7694	0.107	0.300	823	2308
		93	10387	0	0	0	0
		94	2473	0	0.273	0	675
		95	3297	0	0.072	0	237
	D	96	73	0	0.167	0	12
		97	146	0	0.020	0	2
		98	0	0	0	0	0
		99	170	0	0.273	0	46
1981	J	100	512	0	0.100	0	51
		101	0	0	0	0	0

Dictyosphaerium ehrenbergianum

Year	Month	Week	Host Cells/ml	Fraction of Zoospores	Fraction of Dead Hosts	Zoospores Cells/ml	Dead Hosts Cells/ml
1979	J	1	0	0	0	0	0
		2	0	0	0	0	0
	F	3	0	0	0	0	0
		4	0	0	0	0	0
		5	0	0	0	0	0
		6	0	0	0	0	0
	M	7	0	0	0	0	0
		8	0	0	0	0	0
		9	0	-	-	-	-
		10	0	0	0	0	0
	A	11	0	0	0	0	0
		12	0	0	0	0	0
		13	0	0	0	0	0
		14	0	0	0	0	0
	M	15	0	0	0	0	0
		16	0	0	0	0	0
		17	0	-	-	-	-
		18	0	0	0	0	0
		19	0	0	0	0	0
	J	20	0	0	0	0	0
		21	0	0	0	0	0
		22	0	0	0	0	0
		23	0	-	-	-	-
	J	24	0	0	0	0	0
		25	0	0	0	0	0
		26	0	0	0	0	0
		27	0	0	0	0	0
	A	28	9364	0	0.023	0	.215
		29	23183	0	0	0	0
		30	0	0	0	0	0
		31	0	0	0	0	0
		32	0	0	0	0	0
	S	33	0	0	0	0	0
		34	0	0	0	0	0
		35	0	0	0	0	0
		36	0	0	0	0	0
	O	37	0	-	-	-	-
		38	0	0	0	0	0
		39	0	-	-	-	-
		40	0	0	0	0	0
		41	0	0	0	0	0
	N	42	0	0	0	0	0
		43	0	0	0	0	0
		44	0	0	0	0	0
		45	0	0	0	0	0
	D	46	0	0	0	0	0
		47	0	-	-	-	-
		48	0	0	0	0	0

Dictyosphaerium ehrenbergianum

Year	Month	Week	Host Cells/ml	Fraction of Zoospores	Fraction of Dead Hosts	Zoospores Cells/ml	Dead Hosts Cells/ml
1980	J	49	0	0	0	0	0
		50	0	-	-	-	-
		51	0	0	0	0	0
		52	0	0	0	0	0
	F	53	0	0	0	0	0
		54	0	-	-	-	-
		55	0	-	-	-	-
		56	0	0	0	0	0
	M	57	0	0	0	0	0
		58	0	0	0	0	0
		59	0	-	-	-	-
		60	0	0	0	0	0
		61	0	-	-	-	-
	A	62	0	0	0	0	0
		63	0	0	0	0	0
		64	3590	0	0	0	0
		65	0	-	-	-	-
	M	66	0	0	0	0	0
		67	0	0	0	0	0
		68	0	-	-	-	-
		69	0	0	0	0	0
	J	70	0	0	0	0	0
		71	0	0	0	0	0
		72	0	-	-	-	-
		73	0	0	0	0	0
	J	74	4616	0	0	0	0
		75	3957	0	0	0	0
		76	18467	1.000	0.765	18467	14127
		77	0	0	0.625	0	0
		78	403970	0	0	0	0
	A	79	0	-	-	-	-
		80	17313	0	0	0	0
		81	0	0	0	0	0
		82	15389	0.016	0.060	246	923
	S	83	0	0	0	0	0
		84	0	0	0	0	0
		85	28855	0	0	0	0
		86	0	0	0	0	0
	O	87	0	0	0	0	0
		88	6155	0	0	0	0
		89	0	0	0	0	0
		90	0	0	0	0	0
		91	3297	0	0	0	0
	N	92	15389	0	0	0	0
		93	6925	0	0	0	0
		94	6595	0	0	0	0
		95	2198	0	0	0	0
	D	96	0	0	0	0	0
		97	806	0	0	0	0
		98	5129	0	0	0	0
		99	683	0	0	0	0
1981	J	100	2479	0	0	0	0
		101	153	0	0	0	0

Pteromonas angulosa

Year	Month	Week	Host Cells/ml	Fraction of Zoospores	Fraction of Dead Hosts	Zoospores Cells/ml	Dead Hosts Cells/ml
1979	J	1	0	0	0	0	0
		2	122	0	0.071	0	8
	F	3	926	0	0	0	0
		4	730	0	0	0	0
		5	382	0	0	0	0
		6	57	0	0	0	0
	M	7	149	0	0.500	0	74
		8	0	0	1.000	0	0
		9	0	-	-	-	-
		10	0	0	0.375	0	0
	A	11	614	0	0.500	0	307
		12	0	0	0	0	0
		13	0	0	1.000	0	0
		14	0	0	0.100	0	0
	M	15	0	0	0	0	0
		16	183	0	0	0	0
		17	3684	-	-	-	-
		18	0	0	0.587	0	0
		19	0	0.235	0.083	0	0
	J	20	0	0	0.167	0	0
		21	9169	0.183	0	1678	0
		22	9169	0.173	0	1586	0
		23	1238	-	-	-	-
	J	24	0	0.875	0.330	0	0
		25	0	0.200	0.167	0	0
		26	0	0	0	0	0
		27	0	0	0.200	0	0
	A	28	0	0	0	0	0
		29	0	0	0	0	0
		30	0	0	0	0	0
		31	0	0	0	0	0
		32	0	0	0	0	0
	S	33	0	0	0	0	0
		34	0	0	0	0	0
		35	0	0	0	0	0
		36	0	0	0	0	0
	O	37	0	-	-	-	-
		38	0	0	1.000	0	0
		39	0	-	-	-	-
		40	0	1.000	0	0	0
		41	0	0.600	0.167	0	0
	N	42	908	0	0	0	0
		43	266	0	0	0	0
		44	0	0	0	0	0
		45	0	0	0	0	0
	D	46	0	0	0	0	0
		47	79	-	-	-	-
		48	0	0	0	0	0

Pteromonas angulosa

Year	Month	Week	Host Cells/ml	Fraction of Zoospores	Fraction of Dead Hosts	Zoospores Cells/ml	Dead Hosts Cells/ml
1980	J	49	0	0	1.000	0	0
		50	0	-	-	-	-
		51	0	0	0	0	0
		52	0	0	0	0	0
	F	53	0	0	0	0	0
		54	0	-	-	-	-
		55	0	-	-	-	-
		56	0	0	0	0	0
	M	57	0	0	0	0	0
		58	0	0	0	0	0
		59	0	-	-	-	-
		60	0	0	0	0	0
	A	61	0	-	-	-	-
		62	0	0	0	0	0
		63	0	0	0	0	0
		64	0	0	0	0	0
		65	0	-	-	-	-
	M	66	0	0	0	0	0
		67	0	0	0	0	0
		68	0	0	0	-	-
		69	0	0	0	0	0
	J	70	0	0	0	0	0
		71	0	0	0	0	0
		72	0	-	-	-	-
		73	0	0	0	0	0
	J	74	0	0	0	0	0
		75	0	0	0	0	0
		76	0	0	0	0	0
		77	0	0	0	0	0
		78	0	0	0	0	0
	A	79	0	-	-	-	-
		80	0	0	0	0	0
		81	0	0	0	0	0
		82	0	0	0	0	0
		83	0	0	0	0	0
		84	0	0	0	0	0
		85	0	0	0	0	0
		86	0	0	0	0	0
	S	87	0	0	0	0	0
		88	0	0	0	0	0
		89	0	0	0	0	0
		90	577	0	0	0	0
		91	0	0	0	0	0
	O	92	961	0	0	0	0
		93	0	0	0	0	0
		94	0	0	0	0	0
		95	0	0	0	0	0
	N	96	0	0	0	0	0
		97	0	0	0	0	0
		98	0	0	0	0	0
		99	0	0	0	0	0
1981	J	100	0	0	0	0	0
		101	0	0	0.500	0	0

Pteromonas sp.

Year	Month	Week	Host Cells/ml	Fraction of Zoospores	Fraction of Dead Hosts	Zoospores Cells/ml	Dead Hosts Cells/ml
1979	J	1	0	0	0.091	0	0
		2	0	0	0	0	0
	F	3	0	0	0	0	0
		4	0	0	0	0	0
		5	0	0	0	0	0
		6	0	0	0	0	0
	M	7	0	0	0	0	0
		8	139	0	0.933	0	130
		9	0	-	-	-	-
		10	0	0	0	0	0
	A	11	1620	0	0.100	0	162
		12	1958	0	0	0	0
		13	6520	0	1.000	0	6520
		14	2158	0	0.209	0	451
	M	15	1304	0	0.500	0	652
		16	0	0	0	0	0
		17	586	-	-	-	-
		18	7126	0	0.662	0	4717
		19	12633	0	0.067	0	846
	J	20	3178	0	0	0	0
		21	3301	0	0.091	0	300
		22	17972	0	0	0	0
		23	38210	-	-	-	-
	J	24	65662	0	0	0	0
		25	77047	0	0.027	0	2080
		26	80089	0	0.118	0	9450
		27	17954	0	0.200	0	3590
	A	28	7688	0	0.067	0	515
		29	4651	0	0.167	0	776
		30	13783	0	0	0	0
		31	4730	0	0	0	0
		32	892	0	1.000	0	892
	S	33	0	0	0.250	0	0
		34	0	0	0	0	0
		35	0	0	0	0	0
		36	0	0	0	0	0
	O	37	0	-	-	-	-
		38	0	0	0	0	0
		39	0	-	-	-	-
		40	366	0	0	0	0
		41	652	0	0	0	0
	N	42	419	0	0	0	0
		43	209	0	0	0	0
		44	2934	0	0	0	0
		45	154	0	0	0	0
	D	46	124	0	0	0	0
		47	0	-	-	-	-
		48	0	0	0	0	0

Pteromonas sp.

Year	Month	Week	Host Cells/ml	Fraction of Zoospores	Fraction of Dead Hosts	Zoospores Cells/ml	Dead Hosts Cells/ml
1980	J	49	0	0	0	0	0
		50	0	-	-	-	-
		51	0	0	1.000	0	0
		52	0	0	0	0	0
	F	53	0	0	0	0	0
		54	0	-	-	-	-
		55	0	-	-	-	-
		56	0	0	0	0	0
	M	57	0	0	0	0	0
		58	0	0	0	0	0
		59	0	-	-	-	-
		60	1399	0	0	0	0
	A	61	303	-	-	-	-
		62	213	0	0	0	0
		63	1481	0	0	0	0
		64	5899	0.057	0.011	336	64
		65	1052	-	-	-	-
	M	66	0	0	0.095	0	0
		67	216	0	1.000	0	216
		68	0	-	-	-	-
		69	0	0	0	0	0
	J	70	0	0	0	0	0
		71	0	0	0	0	0
		72	0	-	-	-	-
		73	0	0	0	0	0
	J	74	0	0	0	0	0
		75	0	0	0	0	0
		76	1319	0	0	0	0
		77	0	0	0	0	0
		78	0	0	0	0	0
	A	79	0	-	-	-	-
		80	0	0	0	0	0
		81	0	0	0	0	0
		82	0	0	0	0	0
	S	83	0	0	0	0	0
		84	0	0	0	0	0
		85	0	0	0	0	0
		86	0	0	0	0	0
	O	87	0	0	0	0	0
		88	0	0	0	0	0
		89	0	0	0	0	0
		90	0	0	0	0	0
		91	0	0	0	0	0
	N	92	0	0	0	0	0
		93	0	0	0	0	0
		94	0	0	0	0	0
		95	0	0	0	0	0
	D	96	0	0	0	0	0
		97	0	0	0	0	0
		98	0	0	0	0	0
		99	0	0	0	0	0
1981	J	100	0	0	0	0	0
		101	0	0	0	0	0

Chlamydomonas pertusa

Year	Month	Week	Host Cells/ml	Fraction of Zoospores	Fraction of Dead Hosts	Zoospores Cells/ml	Dead Hosts Cells/ml
1979	J	1	6143	0	0	0	0
		2	2353	0	0	0	0
	F	3	3849	0	0	0	0
		4	2525	0	0	0	0
		5	1484	0	0	0	0
		6	1819	0	0	0	0
	M	7	3134	0	0	0	0
		8	1943	0	0	0	0
		9	3930	-	-	-	-
		10	2433	0	0	0	0
	A	11	7768	0	0	0	0
		12	10359	0	0	0	0
		13	17669	0	0	0	0
		14	6551	0	0	0	0
	M	15	293	0	0	0	0
		16	400	0	0	0	0
		17	880	-	-	-	-
		18	838	0	0	0	0
		19	1047	0	0	0	0
	J	20	183	0	0	0	0
		21	733	0	0	0	0
		22	1956	0	0	0	0
		23	0	-	-	-	-
	J	24	1825	0	0	0	0
		25	1089	0	0	0	0
		26	0	0	0	0	0
		27	0	0	0	0	0
	A	28	0	0	0	0	0
		29	0	0	0	0	0
		30	0	0	0	0	0
		31	0	0	0	0	0
		32	0	0	0	0	0
	S	33	0	0	0	0	0
		34	0	0	0	0	0
		35	0	0	0	0	0
		36	0	0	0	0	0
	O	37	0	-	-	-	-
		38	0	0	0	0	0
		39	0	-	-	-	-
		40	5868	0	0	0	0
		41	13204	0	0	0	0
	N	42	20260	0	0	0	0
		43	17129	0	0	0	0
		44	92429	0	0	0	0
		45	17887	0	0	0	0
	D	46	2542	0	0	0	0
		47	394	-	-	-	-
		48	204	0	0	0	0

Chlamydomonas pertusa

Year	Month	Week	Host Cells/ml	Fraction of Zoospores	Fraction of Dead Hosts	Zoospores Cells/ml	Dead Hosts Cells/ml
1980	J	49	41	0	0	0	0
		50	0	-	-	-	-
		51	56	0	0	0	0
		52	0	0	0	0	0
	F	53	102	0	0	0	0
		54	0	-	-	-	-
		55	839	-	-	-	-
		56	2849	0	0	0	0
	M	57	16690	0	0	0	0
		58	871	0	0	0	0
		59	0	-	-	-	-
		60	4197	0	0	0	0
	A	61	10478	-	-	-	-
		62	5343	0	0	0	0
		63	4445	0	0	0	0
		64	5386	0.044	0	236	0
		65	8944	-	-	-	-
	M	66	5606	0	0	0	0
		67	4833	0.025	0	120	0
		68	3077	-	-	-	-
		69	577	0	0	0	0
	J	70	1615	0	0	0	0
		71	0	0	0	0	0
		72	0	-	-	-	-
		73	2130	0	0	0	0
	J	74	0	0	0	0	0
		75	1319	0	0	0	0
		76	2308	0	0	0	0
		77	0	0	0	0	0
		78	0	0	0	0	0
	A	79	0	-	-	-	-
		80	0	0	0	0	0
		81	0	0	0	0	0
		82	0	0	0	0	0
	S	83	0	0	0	0	0
		84	0	0	0	0	0
		85	0	0	0	0	0
		86	0	0	0	0	0
	O	87	0	0	0	0	0
		88	0	0	0	0	0
		89	0	0	0	0	0
		90	0	0	0	0	0
		91	0	0	0	0	0
	N	92	0	0	0	0	0
		93	0	0	0	0	0
		94	0	0	0	0	0
		95	549	0	0	0	0
	D	96	73	0	0	0	0
		97	0	0	0	0	0
		98	0	0	0	0	0
		99	0	0	0	0	0
1981	J	100	85	0	0	0	0
		101	38	0	0	0	0

Chlamydomonas ovata

Year	Month	Week	Host Cells/ml	Fraction of Zoospores	Fraction of Dead Hosts	Zoospores Cells/ml	Dead Hosts Cells/ml
1979	J	1	15097	0.005	0.005	75	75
		2	9726	0	0	0	0
	F	3	11007	0	0	0	0
		4	6959	0	0	0	0
		5	1838	0	0	0	0
		6	1928	0	0	0	0
	M	7	864	0	0	0	0
		8	34226	0	0	0	0
		9	78032	-	-	-	-
		10	181780	[0.0001]	[0.0005]	[28]	[84]
	A	11	24897	[0.014]	[0.008]	[343]	[193]
		12	11717	0	0	0	0
		13	1630	0	[0.017]	0	[28]
		14	2195	0	0	0	0
	M	15	2538	0	0	0	0
		16	3054	0	0	0	0
		17	880	-	-	-	-
		18	4191	0	0	0	0
		19	4864	0	0	0	0
	J	20	13998	0	0	0	0
		21	42546	0	0	0	0
		22	22618	0	0	0	0
		23	0	-	-	-	-
	J	24	0	0	0	[544]	[272]
		25	21890	0	[0.061]	0	[1330]
		26	17454	0	[0.089]	0	[1548]
		27	45655	0	[0.047]	0	[2137]
	A	28	41824	0	0	0	0
		29	25158	0	0	0	0
		30	7984	0	0	0	0
		31	5940	0	[0.131]	0	[778]
		32	1591	0	0	0	0
	S	33	0	0	0	0	0
		34	0	0	0	0	0
		35	99974	0	0	0	0
		36	0	0	0	0	[300]
	O	37	0	-	-	-	-
		38	0	0	0	0	0
		39	4376	-	-	-	-
		40	19586	0	[0.026]	0	[516]
		41	0	0	0	0	[483]
	N	42	0	0	0	0	0
		43	0	0	0	0	0
		44	0	0	0	[1069]	0
		45	0	0	0	0	0
	D	46	0	0	0	0	0
		47	0	-	-	-	-
		48	0	0	0	0	0

Chlamydomonas ovata

Year	Month	Week	Host Cells/ml	Fraction of Zoospores	Fraction of Dead Hosts	Zoospores Cells/ml	Dead Hosts Cells/ml
1980	J	49	0	0	0	0	0
		50	0	-	-	-	-
		51	24	0	0	0	0
		52	0	0	0	0	0
	F	53	0	0	0	[15]	[25]
		54	0	-	-	-	-
		55	65474	-	-	-	-
		56	48258	[0.078]	0.011	[3746]	[540]
	M	57	20219	0.093	0.048	1880	970
		58	31882	0	0	0	0
		59	21183	-	-	-	-
		60	66314	0.010	0	663	0
	A	61	33866	-	-	-	-
		62	12396	0	0	0	0
		63	23938	0	0	0	0
		64	22058	0	0	0	0
		65	68659	-	-	-	-
	M	66	84091	0.016	0.016	1345	1345
		67	15798	0.164	0.006	2590	94
		68	100030	-	-	-	-
		69	170821	0	0	0	0
	J	70	29316	0.018	0.061	527	1788
		71	29121	0.006	0.022	174	640
		72	44538	-	-	-	-
		73	55401	0.007	0	387	0
	J	74	26546	0.024	0.024	637	637
		75	91016	0	0.057	0	5187
		76	126962	0	0	0	0
		77	0	0	0	0	0
		78	0	0	0	0	0
	A	79	0	-	-	-	-
		80	0	0	0	0	0
		81	0	0	0	0	0
		82	0	0	0	0	0
	S	83	0	0	0	0	0
		84	0	0	0	0	0
		85	1923	0	0	0	0
		86	2051	0	0	0	0
	O	87	36068	0	0	0	0
		88	10772	0	0	0	0
		89	60595	0	0	0	0
		90	10387	0	0	0	0
		91	22259	0	0	0	0
	N	92	53862	0	0	0	0
		93	24815	0	0	0	0
		94	17313	0	0	0	0
		95	4946	0	0	0	0
	D	96	73	0	0	0	0
		97	146	0	0	0	0
		98	2667	0	0	0	0
		99	1880	0	0	0	0
1981	J	100	1453	0	0	0	0
		101	2500	0	0	0	0

Total number of host cells of all species of algae infected by Aphelidium chlorococcarum compared to the total number of zoospores of this parasite on all infected host species.

Year	Month	Week	Total Host Cells/ml	Total Zoospores /ml
1979	J	1	3965	0
		2	3272	8
	F	3	1917	0
		4	2624	0
		5	652	0
		6	1516	0
	M	7	1304	0
		8	1269	0
		9	1637	0
		10	6868	0
	A	11	7681	41
		12	3116	0
		13	11734	48
		14	2442	3
	M	15	2723	38
		16	260	16
		17	6714	0
		18	13411	0
		19	16277	116
	J	20	49330	2215
		21	61983	2828
		22	74453	1922
		23	68168	0
	J	24	107067	7223
		25	134575	4152
		26	167837	0
		27	312401	1267
	A	28	208862	473
		29	577239	0
		30	466115	0
		31	288086	0
		32	131045	0
	S	33	29827	97
		34	644	19
		35	32602	0
		36	46440	310
	O	37	92773	0
		38	373671	3440
		39	221999	0
		40	203562	1541
		41	73437	6314
	N	42	199597	1594
		43	54186	309
		44	165295	1107
		45	26832	108
	D	46	13203	1436
		47	11616	0
		48	4217	0

Year	Month	Week	Total Host Cells/ml	Total Zoospores /ml
1980	J	49	835	6
		50	650	0
		51	887	32
		52	1615	101
	F	53	1126	14
		54	3417	0
		55	0	0
		56	1519	0
	M	57	9033	503
		58	5573	154
		59	180	0
		60	13987	103
	A	61	3793	0
		62	7052	202
		63	1937	0
		64	10514	438
		65	4207	0
	M	66	9232	0
		67	1369	0
		68	3589	0
		69	577	0
	J	70	7846	210
		71	10120	73
		72	39647	0
		73	58239	3099
	J	74	63092	3897
		75	159607	13165
		76	315259	34630
		77	3868	876
		78	1817864	10753
	A	79	544396	-
		80	923359	64322
		81	406855	30018
		82	121188	3571
	S	83	180823	7618
		84	380884	965
		85	413587	8033
		86	222629	2154
	O	87	435708	0
		88	473990	9275
		89	261136	13984
		90	132731	31542
		91	183019	24571
	N	92	153889	15026
		93	113109	3117
		94	107998	2244
		95	69800	978
	D	96	512	0
		97	11136	50
		98	28929	0
		99	9743	40
1981	J	100	13078	304
		101	1921	0