

- Sept. 1937. E. B. Worthington took up duties as first Director.
 April 1938. Coarse Fish Investigation began.
 April 1939. Avon Biological Research became the Association's 'University College, Southampton, Branch for Southern Rivers'.
 June 1940. Branch for Southern Rivers closed.
 June 1940. Part of the Fisheries Lab., Lowestoft, and British Museum (N.H.) evacuated to Wray Castle.
 November 1947. The Ferry House purchased.
 June 1948. Lease of Wraymires hatchery and tarns.
 August 1948. Award of Einar Naumann medal to the Association by Societas Internationalis Limnologiae.
 September 1950. Move from Wray Castle to The Ferry House.
 September 1953. Pollution Research Unit started work.
 April 1957. Purchase of fishing rights at East Stoke.
 December 1963. River Laboratory completed.
 1964. Association began to administer the Royal Society's Lake George IBP project.
 20 May 1965. Formal opening of River Laboratory.
 1 June 1965. Natural Environment Research Council took over from Development Commission responsibility for grant-aiding the Association.
 1 April 1967. Quaternary Research group joined Association's staff.
 March 1969. Work began at Cow Green.
 1969. Purchase of Waterston water-cress beds.
 1970. Midlands Unit established.
 23 July 1971. Formal opening of fluvarium and extension to River Laboratory.
 25 March 1972. Death of G. J. Thompson, Laboratory Steward.
 26 March 1972. Death of F. J. H. Mackereth, Chemist.
 1972. Publication of White Paper, Cmnd 5046, on organisation of government research.
 1 April 1973. Some research projects became commissioned by Department of the Environment and Ministry of Agriculture Fisheries and Food.
 14 April 1973. Formal opening of Pearsall Building.
 1973. End of Royal Society's IBP project on Lake George, Uganda.
 Summer 1977. Teesdale Unit established.
 September 1977. Formal opening of Meeting Room at River Laboratory.
 October 1978. Completion of purchase of West Holme fishing rights on River Frome.
 March 1979. Completion of conversion of Stoke Mill Farm House into laboratories.

FUNGAL AND PROTOZOAN PARASITES AND THEIR IMPORTANCE IN THE ECOLOGY OF THE PHYTOPLANKTON

HILDA M. CANTER (Mrs J. W. G. LUND)

Fungi and protozoa responsible for the death of algae, more especially non-planktonic forms, were first described by the early European microscopists. Many excellent observations and illustrations were made by these workers in an era between the mid-19th and early 20th centuries.

During this period, there was no intensive work in Great Britain on these organisms although a few scattered papers do exist in the literature. The first real investigation in this country of the fungi classed as Aquatic Phycomycetes was carried out by the late Dr F. K. Sparrow during his visit to Cambridge in the years of 1932-1933. Even so, species living on the planktonic algae of large lakes received no attention.

It was in 1943 at an FBA botany class that the presence of fungi on the phytoplankton of Windermere was first noted by me and a very striking chytrid saprophyte was found attached to frustules of *Ceratium*. At that time, Professor C. T. Ingold was studying chytrids and so contact was made with him. The fungus on *Ceratium* proved to belong to a new genus which he named *Amphicypellus* Ingold (1944) (Plate 3a). This link with Professor Ingold was eventually to lead to the intensive survey carried out on the fungi which live on planktonic algae in the English Lake District and elsewhere.

Descriptive studies.

The main bulk of the fungal parasites (and saprophytes) associated with the phytoplankton belong to the Chytridiales or are simple biflagellate Phycomycetes. (See Sparrow 1960, Karling 1977). In each group there is a stage in the life-history when numerous minute free-swimming bodies called zoospores are formed. They are the main dispersive agents of these fungi and ultimately they find new algal cells upon which to grow. The chytrid zoospore (Fig. 1A,z) typically possesses a spherical body and contains a single bright refractive globule. The flagellum is posteriorly placed and propels the zoospore from behind. In contrast the zoospore of a simple biflagellate fungus (Fig. 1B,z) is often shaped like a bean or grape seed. It contains several small refractive globules and the two flagella are laterally inserted and oppositely directed when swimming.

Commonly in a chytrid, a fine thread from the adherent encysted zoospore penetrates the algal cell and internally forms a rhizoidal system (Plate 4D). Nourishment is conveyed back to the zoospore which enlarges and becomes a sporangium (Plate 3B). The sporangium matures and further zoospores are produced (Fig. 1A). Liberation of these zoospores takes place by diverse methods of sporangial dehiscence. A part of the wall may form a well-defined operculum (Plate 4C), a few or numerous small

holes may be formed, or a lesser or greater part of the sporangium may dissolve away.

The sporangia of biflagellate fungi are often narrow tubular or sac-like in shape. They do not possess rhizoids and are located within the algal host cell. In many species when the sporangium is fully grown, its content, surrounded by a vesicle, passes out of the alga, via a narrow exit tube. Within this vesicle the zoospores undergo their final maturation and are liberated when it bursts (Fig. 1B; Plate 4A).

The production of thick-walled asexually or sexually formed resting spores occurs in both these groups of fungi (Fig. 1A, C). However, for some frequently encountered species, such a stage has not yet been discovered.

Again, in both groups there exist species which kill algal cells on a one-to-one basis and those in which a single infection will result in the death of many algal cells.

While studying the above fungi it became clear that there abounded in the plankton yet another group of organisms which could utilize algae as a source of food. They were Protozoa similar to species placed in the Proteomyxidia, Monadineae, 'zoosporeae' and 'azoosporeae' by Zopf (1885). The Proteomyxidia is a dumping ground for lowly organisms of unclear taxonomic or phylogenetic position. As such it includes a heterogeneous collection of genera and species. Many are very incompletely known and frequently they have not been recorded since their original collection. The diversity of their life-cycles seems unending and several distinct anatomical stages are usually present in any one animal. Among such stages are trophic amoebae, posteriorly uniflagellate zoospores, anteriorly biflagellate swimmers which divide by binary fission, and special cysts which serve not only for the digestion of algal materials but also for multiplication or resting-spore formation. The most familiar generic name belonging to such Protozoa is likely to be *Vampyrella*.

One protozoan, sometimes referred to as a chytrid, which frequently destroys small unicellular or colonial green algae belongs to the genus *Aphelidium* (Plate 3C). It forms posteriorly uniflagellate zoospores which externally resemble those of chytrids. After the zoospore has settled on an algal cell its content passes inside, where it gradually ingests the chromatophore material. Within the algal cell a new crop of zoospores is produced. After their release all that remains is a small red or brownish sphere of undigested algal material.

The feeding stages of biflagellate species such as the *Pseudosporae* or the amoeboid *Vampyrellas* (Fig. 1G; Plate 4B) attach themselves directly to an algal cell or make pseudopodial contact from a distance. Frequently a hole is then made in the algal wall. In some species the entire content of an algal cell flows out rapidly into the animal's body whereas, in others, it may be sucked out as small pieces over a longer period of time.

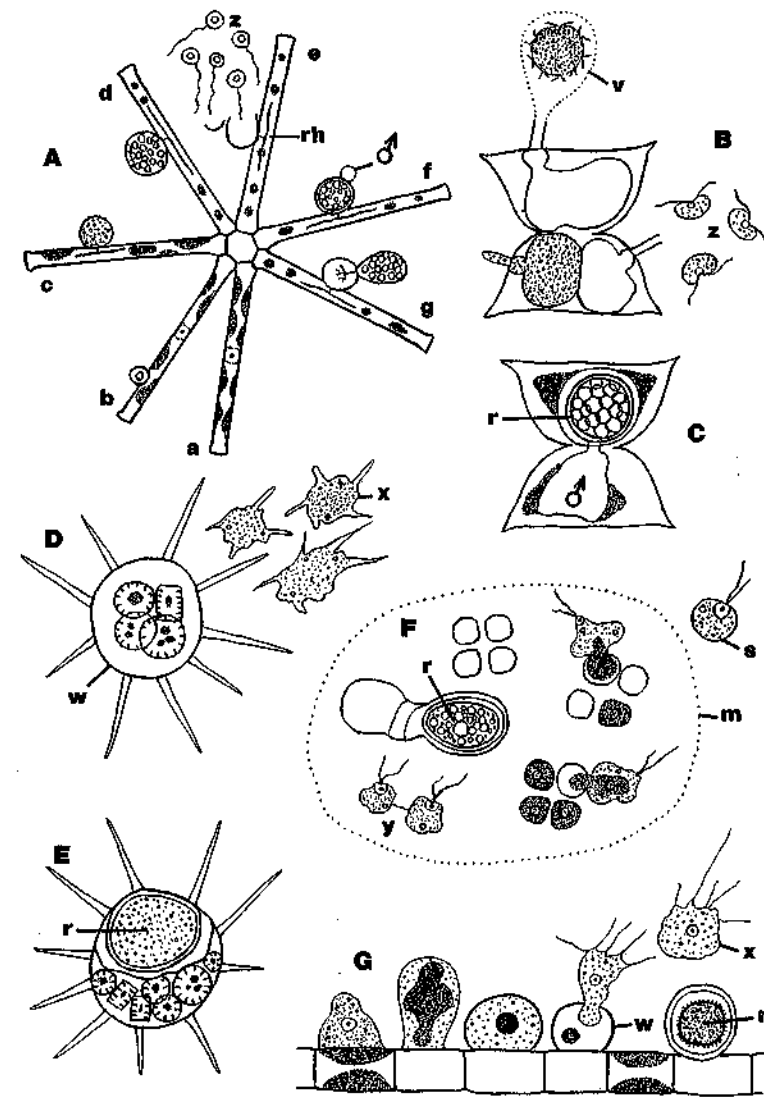


FIG. 1. Representative stages in the life cycles of some fungi and protozoa parasitic on planktonic algae (free-hand sketches).

- A A chytrid on *Asterionella*. Cell (a) uninfected, (b) with an encysted zoospore, (c) immature sporangium, (d) mature sporangium, (e) empty operculate sporangium, (f) resting spore, (g) sporangium with external hyperparasite.
 B-C A biflagellate fungus in a desmid: B, sporangia and dehiscence; C, resting spore.
 D-E *Asterocaelum* cysts with residues of centric diatoms: D, cyst from which three amoebae have emerged; E, cyst containing a resting spore.
 F The biflagellate protozoan *Pseudospora*, within a colony of the green alga *Gemellicystis*. The trophic amoeba stage ingests the content of individual cells.
 G A *Vampyrella* which 'sucks out' the content of *Ulothrix*-like algae.

Legend. *m*, mucilage envelope; *r*, resting spore; *rh*, rhizoid; *s*, biflagellate swimmer; *v*, dehiscence vesicle; *w*, cyst wall; *x*, non-flagellate amoeboid stage; *y*, binary fission; *z*, zoospore.

The amoeboid organism *Asterocaelum algophilum* Canter (1973) possesses long tapering pseudopodia which wave to and fro. It captures mainly small centric diatoms which are then ingested whole. In both *Vampyrella* (Fig. 1G) and *Asterocaelum* (Fig. 1D) special cysts are formed in which digestion of the algal material takes place. The animal then re-emerges as one or more individuals and the undigested algal residues are left behind. At other times, the content of a cyst becomes transformed into a solitary resting spore (Fig. 1E).

There is also ample evidence that many other types of Protozoa live on planktonic algae. Quantitatively, their effects on algal populations have received little attention. What may be termed free-living or true amoebae, as well as the ciliate *Nassula*, are often found feeding on the cells of blue-green algae.

Both the chytrids and biflagellate fungi may themselves become parasitized by other fungi called hyperparasites. Where the main sporangium of a chytridiaceous hyperparasite is located on the external surface of its host, its presence is immediately noted (Fig. 1A, g). However, other hyperparasite species invade and develop entirely within the host fungus. Since colourless protoplasm is common to both parasite and hyperparasite, such a situation as this is not always easily detected. It often comes to light when the 'wrong' kind of zoospore is seen to emerge from a sporangium, or the 'wrong' type of dehiscence takes place.

In the latter case hyperparasitism could lead to misidentification. Two small globular chytrids *Zygorhizidium affluens* Canter and *Z. planktonicum* Canter can be found occurring simultaneously on a population of *Asterionella*. Although they are both operculate (dehiscence by a lid), their empty sporangia should be instantly distinguishable. In the former species the empty sporangium possesses a wide lateral, rarely apical, opening whereas in the latter there is a narrow apical opening. However, when *Z. affluens* is parasitized by *Rozella parva* Canter a small apical opening is produced. Such a sporangium now resembles the normal empty sporangia of *Z. planktonicum*. Rhizoidal differences do exist between these species. However at this late stage when the rhizoids are empty, they may be very difficult, if not impossible, to observe.

For a considerable proportion of the years between 1948 and 1973, samples from Windermere, Blelham Tarn and Esthwaite Water have been examined on a weekly basis and the presence of fungi recorded. In the more recent years records of the protozoan parasites were also kept. Such long-term observations are, I believe, unique. Some parasites occur with great regularity each year and can be found over a period of months. Others may occur just as regularly but last only a couple of weeks. Yet others may 'disappear' over a period of years, although the host alga has remained just as common. Alternatively, when a new alga enters a lake and establishes itself, a hitherto unrecorded parasite may soon

appear. Many of the parasites, at least in these lakes, appear to be highly specific to a single or a small range of related algal species.

In Windermere alone there are over sixty known (although not all described) fungi and protozoa. The greatest number seen on any one day occurred in August 1970 when twenty-four different species were recorded. It is thought by some that Windermere is peculiar. Perhaps due to its varied algal flora it does possess abundant parasites but it is not unique. Isolated samples and others collected over longer periods have been examined from many parts of the world. In them a wealth of known or new fungal and protozoan pests of algae have been found.

Dr Sparrow has admirably summed up the study of chytrids (and for that matter protozoan parasites). I quote, "I need not repeat the harsh words uttered in the past about these dazzling and elusive creatures. Their epithets have been multitudinous, vigorously expressed and usually justified. Chytrids are minute, here today and gone tomorrow, recalcitrant wherever and whenever the opportunity offers and all in all thoroughly uncooperative. They have left generations of skilled mycologists wondering in their final hours if they really had seen such and such a chytrid forty years ago, for it had never afterwards been seen".

Epidemics

In the study of lakes, limnologists for many years concentrated more or less exclusively on the physico-chemical factors responsible for alterations in numbers of the phytoplankton. The possible importance of a biological factor such as parasitism remained unexplored.

It was in this field that collaboration with Dr J. W. G. Lund opened up a new approach. It has now been demonstrated beyond question that fungal and protozoan epidemics occur in lakes and at times represent a significant factor in the decline of algal populations.

The earliest work centred around the diatoms *Asterionella* and *Fragilaria* which are parasitized by chytrids (Canter & Lund 1953). Later investigations (Canter & Lund 1969) showed that the desmid populations in Windermere may be controlled to a large extent by fungal epidemics. The desmid species are rather similar in their ecology and despite frequent parasitism they increase as a whole each summer. Nevertheless parasitism can have a fundamental effect on which species predominates over this summer period. The desmids are parasitized by both chytrids and biflagellate fungi but the latter group appears more effective in this respect.

We also studied the influence Protozoa had on the phytoplankton. Among colonial green algae e.g. *Dictyosphaerium*, *Eudorina*, *Gemelliscystis*, *Paulschulzia* and *Sphaerocystis*, as well as certain ulotrichine algae, the effects of protozoan infestations could be dramatic. This was not only in terms of severity but also rapidity (Canter & Lund 1968). In most cases only about two weeks were needed for the parasites to ingest the content of

about 99% of the algal cells. This short period, of whatever one likes to call it – ‘parasitism’ or ‘grazing’ – is probably one of the main reasons why these organisms have been overlooked. It is clear that unless there is weekly or at the most fortnightly sampling of a lake, their presence may be completely missed and there may be no clue as to what has happened to a particular algal population. Indeed, frequently all that is left of a colonial green alga is its mucilage envelope and this will remain quite invisible unless the sample has been placed in Indian ink before examination.

Culture work

Obviously a logical extension of any observations on natural populations is an attempt to culture and then experiment with these organisms in the laboratory.

Among the Protozoa, a species of *Pseudospora* whose food is *Gemelliscystis*, the *Vampyrella* which lives off certain planktonic *Ulothrix*-like algae, and *Asterocaelum algophilum* have all been brought into dual clone culture by Dr J. W. G. Lund. They were maintained for periods exceeding a year and studied mainly in relation to the variety of the algal species and content which they could devour.

In 1958 Miss J. Hughes (Mrs Bott) had some success with the biflagellate fungus *Myzocyttium*. On several occasions it grew well enough to destroy her cultures of the desmid *Cosmarium*.

Dr Lund tried unsuccessfully to culture chytrids on planktonic diatoms in 1947, but in the past few years three have been isolated and brought into uni-algal, uni-fungal clone culture by Mr G. Jaworski. They are currently being maintained by him in dual clone culture and all have already survived in this manner for not less than 2½ years.

Most of the experimental work in this connection has been undertaken with an isolate of the species *Rhizophyidium planktonicum* Canter emend., clone C2, from Rydal Water, which parasitizes *Asterionella* (Canter & Jaworski 1978). Clones of this diatom collected from various geographical localities, i.e. England, Wales, Italy, Poland, Canada and U.S.A., have been found suitable for the successful growth and increase (over 90% infection) of this fungus in the laboratory. Although zoospores can encyst on dead *Asterionella* cells we found no evidence to suggest that the chytrid could complete its life history on such dead material.

In cross inoculations with other diatoms very rare sporangia were found which had developed on *Fragilaria* and *Synedra*. However no apparent increase in infection took place on these diatoms and the fungus died out. Zoospores which had encysted on *Tabellaria* and *Cyclotella* were rarely encountered. They died without further growth and the live host cells remained unaltered.

Once contact has been made with an algal cell and germination and

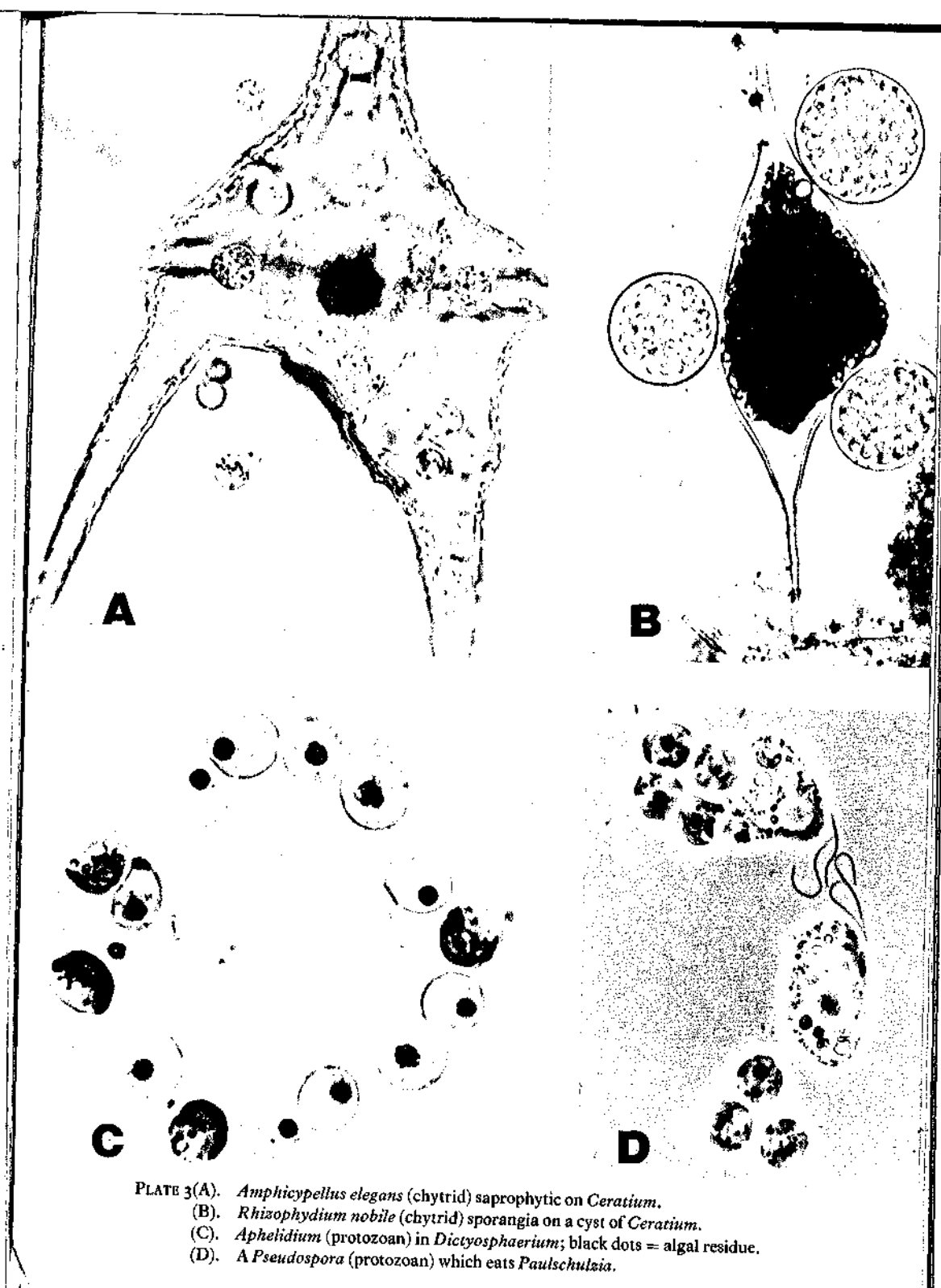


PLATE 3(A). *Amphicypellus elegans* (chytrid) saprophytic on *Ceratium*.
 (B). *Rhizophyidium nobile* (chytrid) sporangia on a cyst of *Ceratium*.
 (C). *Aphelidium* (protozoan) in *Dictyosphaerium*; black dots = algal residue.
 (D). A *Pseudospora* (protozoan) which eats *Paulschulzia*.

infection have taken place, the successful chytrid parasite needs conditions whereby it can grow into a sporangium and produce zoospores. The latter will then infect new host cells. Apart from any environmental factors, it is important to have a compatible nutritional relationship with the host cell and the majority of cells in the algal population must fulfil this requirement. In *Asterionella*, compatible host cells can remain alive over 24 hours until the fungal sporangium is well enlarged, perhaps even fully grown.

The hypersensitive response, whereby incompatible plant cells react rapidly to the presence of a fungus and die, is well documented among the parasites of higher plants. That a similar reaction can also take place between a chytrid and an alga now seems certain (Canter & Jaworski 1979). Cultures of a Canadian clone of *Asterionella* were inoculated with zoospores of *R. planktonicum* emend. Within a matter of 8-12 hours it was found that many of the cells upon which a zoospore had encysted possessed either disorganized contents or had already died. By 24 hours after inoculation frequently over 90% of the cells bearing an encysted zoospore were dead. Instead of developing into a crop of growing sporangia these zoospores remained unexpanded and there was no evidence of the normal long thread-like rhizoid which develops inside a compatible host cell. Under such circumstances it was impossible to prove by conventional microscopy that some rhizoidal contact between the fungus and the diatom cytoplasm had definitely taken place. However a minute rod-like rhizoidal process was noted which appeared to be within the diatom cell. Like the *Asterionella* cells upon which they had encysted, these zoospores also died.

In rare instances cells were found which had presumably reacted in a less sensitive manner and development beyond the zoospore stage had taken place on them. Just twenty such cells were noted in our many experiments, whereas the majority which became infected (4000+) in this particular Canadian clone behaved in an incompatible hypersensitive manner.

Such a reaction acts as a form of resistance for a higher plant but it is of no protection for a single algal cell. Nevertheless it would appear to protect the algal population as a whole. Even when inoculation via a zoospore suspension resulted in great initial cell mortality of the Canadian *Asterionella* clone, the population soon recovered and grew once more into a dense healthy culture.

It is clear that the cultivation of phytoplankton pests is possible although great patience may be required. The chytrid *Zygorhizidium affluens* Canter, a parasite of *Asterionella*, defied many attempts. In nature it is frequently parasitized by the internal chytrid parasite *Rozella*. As a result, not only can the population of the host fungus (i.e. the one being isolated) be reduced at the enrichment stage but in the final isolation, using an inverted microscope with a relatively low-power magnification, it would be quite impossible to tell whether the individual sporangium was infected or not. Again, as exemplified by *R. planktonicum*, a host clone whose cells at least in

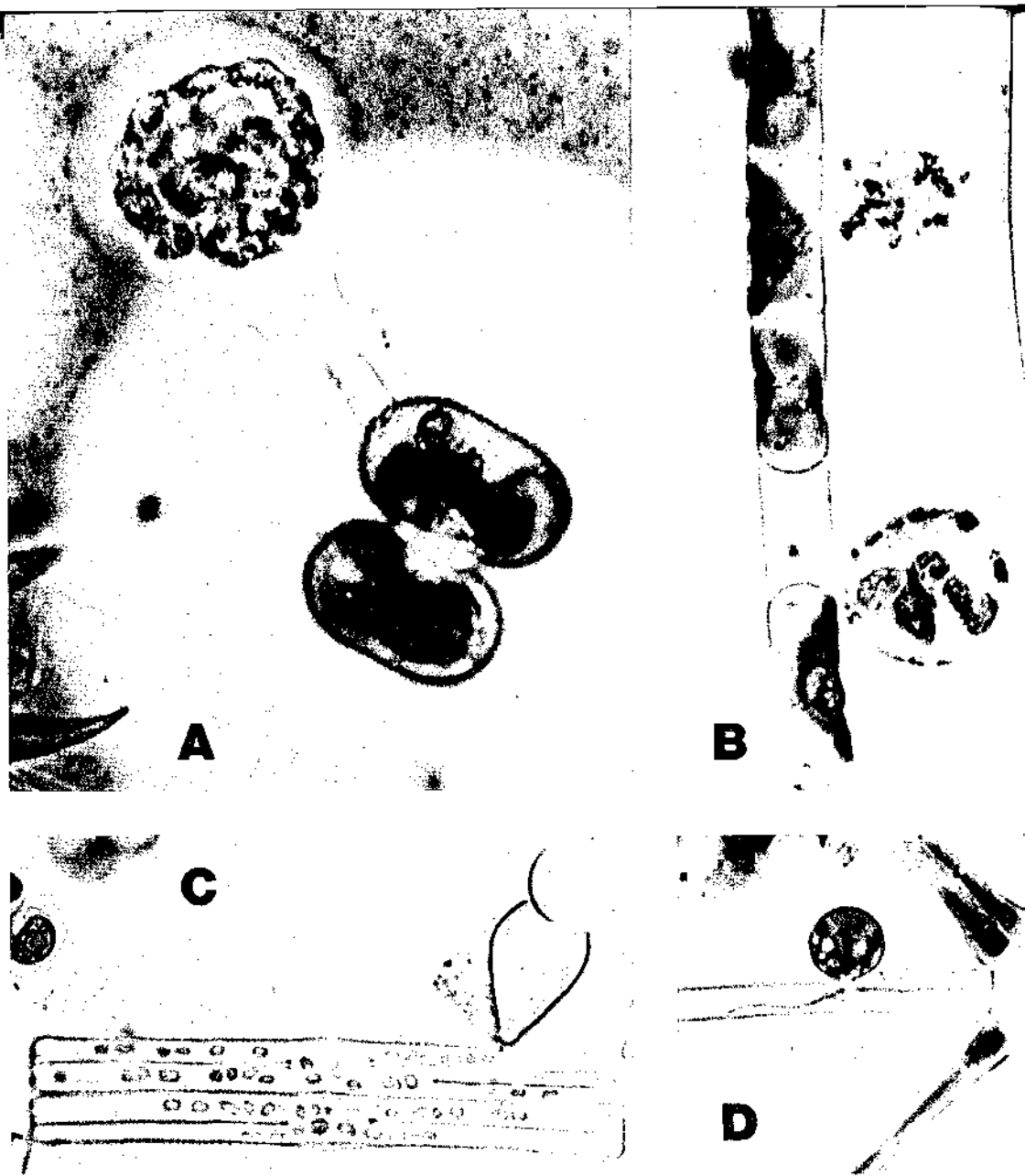


PLATE 4(A). Dehiscence of a biflagellate fungus in *Cosmarium*; out of focus (left) a chytrid saprophyte.
 (B). *Vampyrella* (protozoan) ingesting cell content of a green filamentous alga.
 (C). *Chytridium versatile* (chytrid) on *Tabellaria*; empty sporangium with operculum.
 (D). *Zygorhizidium affluens* (chytrid) rhizoid inside an *Asterionella* cell.

the majority are compatible to fungal development, must be used in the final isolation.

Unicellular organisms offer many advantages in the study of intimate relationships between host and parasite. Already such lines of investigation between the algae (diatoms) and their parasites (chytrids) have revealed valuable information.

I wish to thank all those people, too numerous to mention individually, who have collected and sent me plankton samples or assisted in other ways. I am deeply grateful to Dr J. W. G. Lund and Professor C. T. Ingold for all the help and encouragement they have so kindly given during this investigation.

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ASPECTS OF THE BIOLOGY OF COARSE FISH IN THE DORSET STOUR

R. H. K. MANN

Introduction

Studies of coarse fish communities in Britain, particularly in rivers, have been few in comparison with investigations of salmonid populations. The Dorset Stour is one of the prime coarse fish rivers in this country, and an investigation of the principal species was carried out from 1968 to 1974. Since 1974 only a single mid-summer survey of the populations has been made each year. This article examines some of the results from five species which are of particular interest to anglers; roach *Rutilus rutilus* (L.), dace *Leuciscus leuciscus* (L.), chub *L. cephalus* (L.), pike *Esox lucius* L. and perch *Perca fluviatilis* L. Most of the results have been presented in five papers (Mann 1973, 1974, 1976a, b, 1978).

The study site and methods of fish capture

The River Stour has several chalk-stream tributaries, but its main drainage is from the Oxford and Kimmeridge clays in the Blackmore Vale on the Dorset-Somerset border. Fluctuations in its discharge are therefore more pronounced than those of rivers, such as the Frome at East Stoke, which arise solely from the chalk aquifer. The water has a high ionic concentration ($545 \mu\text{S cm}^{-1}$, pH 8.0), and the extensive areas of marginal and mid-water plants, principally *Iris*, *Scirpus* and *Ranunculus*, support an

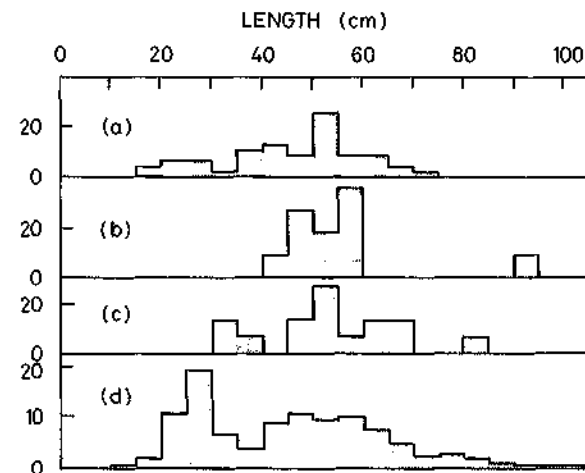


FIG. 1. Length-frequency histograms of pike caught in the River Stour from 1968 to 1978 by (a) Traps (N = 47), (b) Rod (N = 11), (c) Gill net (N = 15) and (d) Electric fishing (N = 415).