British Phycological Journal

ISSN: 0007-1617 (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/tejp19

The effect of attached vorticellids on the buoyancy of the colonial cyanobacterium *Anabaena lemmermannii*

Hilda M. Canter , A.E. Walsby , R. Kinsman & B.W. Ibelings

To cite this article: Hilda M. Canter , A.E. Walsby , R. Kinsman & B.W. Ibelings (1992) The effect of attached vorticellids on the buoyancy of the colonial cyanobacterium *Anabaena lemmermannii* , British Phycological Journal, 27:1, 65-74, DOI: 10.1080/00071619200650081

To link to this article: https://doi.org/10.1080/00071619200650081

Published online: 17 Feb 2007.

Br. phycol. J. **27:** 65–74
1 March 1992

The Effect of Attached Vorticellids on the Buoyancy of the Colonial Cyanobacterium *Anabaena lemmermannii*

By HILDA M. CANTER*, A. E. WALSBY†, R. KINSMAN†, and B. W. IBELINGS‡

**Freshwater Biological Association, The Ferry House, Ambleside, Cumbria LA22 0LP, England; †Department of Botany, University of Bristol, Bristol BS8 1UG, UK; ‡Laboratory of Microbiology, University of Amsterdam, Nieuwe Achtergracht 127, 1018 WS Amsterdam, The Netherlands*

Colonies of the cyanobacterium *Anabaena lemmermannii*, from the southern basin of Windermere in the English Lake district, had heavy infestations of attached vorticellids. The carnivorous ciliates *Trachelius ovum* and *Acaryphrya* sp. were grazing on the vorticellids, and an unidentified parasite was also present. Many of the *Anabaena* colonies appeared to swim, propelled by the action of the attached vorticellids' cilia. In samples left to stand, the majority of the colonies aggregated at the surface. This net upward movement was caused by the buoyancy provided by gas vesicles in the *Anabaena* cells; the colonies sank if the gas vesicles were collapsed by pressure. From measurements of the buoyant density of separated *Anabaena* filaments and detached vorticellids it was calculated that an average colony with a volume of $1{\cdot}3 \times 10^6$ μm^3 would buoy up 103 vorticellids. It was observed that single vorticellids could be buoyed up by filaments with as few as 19 cells.

Filaments and colonies of planktonic cyanobacteria are often seen to be infested by various pathogens, predators (Daft & Stewart, 1971; Canter, 1973; Dryden & Wright, 1987), and other microorganisms. Bacteria also commonly reside within or on the surface of the mucilage envelope that surrounds many of these cyanobacteria, e.g. species of *Gomphosphaeria* (Lund, 1966; Cmiech, Leedale & Reynolds, 1987; Sen, 1988), *Microcystis* and *Anabaena* [Caldwell & Caldwell, 1978; Paerl, 1988; Sen, 1988). In *Anabaena* and *Aphanizomenon* specific associations between bacteria and heterocysts have been noted (Caldwell & Caldwell, 1978; Paerl, 1976, 1982; Paerl & Keller, 1978; Lupton & Marshall, 1981).

Invasion of colonies of *Gomphosphaeria* and *Microcystis* by other cyanobacteria and microalgae has been recorded (Pankow, 1986; Sen, 1988). Protozoans, such as choanoflagellates (Sen, 1988) and peritrichs (ciliata) occur as epibionts, with their stalks embedded in the mucilage envelope or attached to cells. Species of the peritrichs *Vorticella* and *Pseudovorticella* (Warren, 1986, 1987), which concern us here, occur on a wide range of planktonic cyanobacteria. In addition to all the aforementioned genera they have also been reported from *Aphanocapsa, Gloeotrichia, Lyngbya, Nostoc* and *Rivularia* (Kahl, 1935; Davis, 1973; Pace & Orcutt, 1981; Kerr, 1983; Pratt & Rosen, 1983; Canter, Heaney & Lund, 1990).

Canter, Heaney & Lund (1990) observed the frequent occurrence of large numbers of vorticellids, especially *Pseudovorticella molinata* (Tatem) Foissner & Schiffmann attached to colonies of *Anabaena lemmermannii* (P. Richt.) Canab. in the course of studies on the grazing of cyanobacteria by the ciliate *Nassula* in Windermere and some other lakes in Cumbria, England. Similar heavy infestations of cyanobacterial colonies have also been reported by Kerr (1983) on *Nostoc* sp. in Balsam Lake, Wisconsin, USA,

0007–1617/92/010065+10 $03.00/0

by Pratt & Rosen (1983) on *Anabaena flos-aquae* (Lyngb.) de Brébisson in Douglas Lake, Michigan, USA, and by Davis (1973) on *A. flos-aquae* in Bauline Lake, Newfoundland.

Both Kerr (1983) and Pratt & Rosen (1983) record the attachment of several species of *Vorticella* to a variety of cyanobacteria. Kerr (1983) noticed that *Nostoc* sp. was preferentially colonized by all species and found no preferential attachment of one *Vorticella* species to a particular cyanobacterium. Pratt & Rosen (1983), however, describe an exclusive association between *Vorticella* (*Pseudovorticella*) *molinata* and *A. flos-aquae*.

Apparent "swimming" movements exhibited by balls of *Anabaena* with attached vorticellids were reported by Pratt & Rosen (1983) and Canter, Heaney & Lund (1990). Pratt & Rosen (1983) also commented that the vorticellids may contribute to the sinking of a colony.

Colonial planktonic cyanobacteria are buoyed up by their gas vacuoles (Reynolds & Walsby, 1975). They may become sufficiently buoyant that they will float up even when considerable numbers of epibionts are attached to them. In a surface waterbloom the complex association of cyanobacteria with bacteria, microalgae and protozoa may effectively be buoyed up by the flotation provided in this way.

We describe here further observations on the vorticellids associated with colonies of *A. lemmermannii*, which became the dominant phytoplankton species for a short period in Windermere during the summer of 1990. We have investigated the number of vorticellids that a colony can buoy up by making measurements of the buoyant densities of these microorganisms. The swimming movements that result from the feeding currents set up by the vorticellids appear to have no significance in translational motility, but they may have a secondary role as Pratt & Rosen (1983) have suggested.

METHODS

Colonies of *A. lemmermannii* were collected from the southern basin of Windermere with a plankton net, mesh size 65 μm. Samples of a surface waterbloom, formed by the same cyanobacterium in Mitchell Wyke, a small bay behind the Ferry House, were collected with beakers held at the water surface.

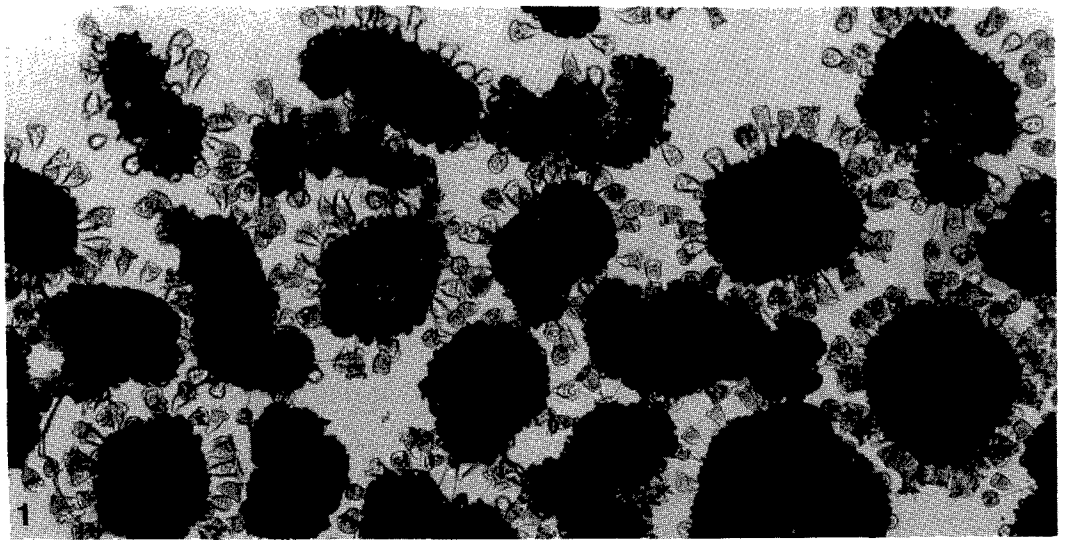
The colonies and vorticellids were examined in microscope counting chambers with a gap of 1 mm between the slide surface and the coverslip, which permitted movement of the colonies. Photomicrographs of live material were taken on a Zeiss Photomicroscope I fitted with an electronic flash device.

The buoyant densities of the vorticellids and the cyanobacterial colonies were determined by centrifugation on concentration gradients of Percoll as described by Oliver, Kinnear & Ganf (1981) and Oliver & Walsby (1988). Concentrated suspensions of the microorganisms in lake water were layered over the preformed Percoll gradients and then centrifuged in a swing-out rotor for 4 min at 4000 rpm, generating an acceleration of 23,800 m s^{-2} (2420 ***g***) in the middle of the gradient. The density of the layers to which the microorganisms sank was determined by dropping samples into calibrated density gradients formed from carbon tetrachloride and paraffin mixtures.

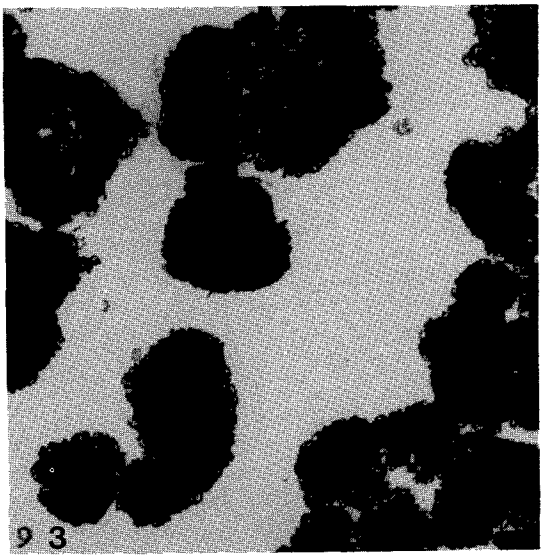
RESULTS

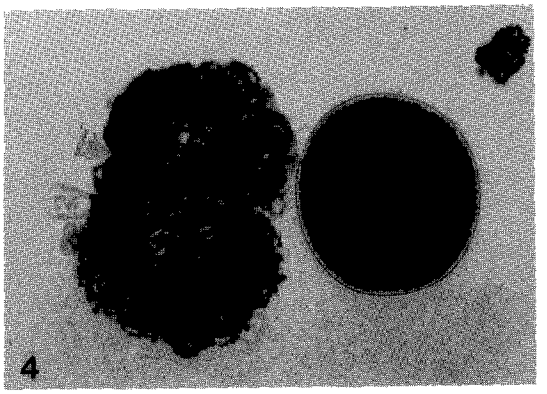
During the week of 18–24 June 1990 colonies of *A. lemmermannii* were abundantly present in the plankton of Windermere. In samples collected from the South Basin on 19 June it was observed that the majority of the colonies of this cyanobacterium were heavily infested by vorticellid peritrichs (Fig. 1), which as previously recorded (Canter, Heaney & Lund, 1990) consisted for the most part of *P. molinata* (Fig. 11). As a result of external influences and the contractile nature of their stalks,

FIGS 1–4. *Anabaena lemmermanni*. Fig. 1. Colonies heavily infested with vorticellids; Windermere, south basin. ×64. Fig. 2. Part of a colony showing vorticellids attached by stalks that are expanded or contracted. ×256. Fig. 3. Colonies virtually devoid of vorticellids from waterbloom, Mitchell Wyke. ×64. Fig. 4. The ciliate grazer *Nassula aurea* (right) filled with cells of *Anabaena*. ×110.


1


2


3


4

individual peritrichs exhibited positions of extension or contraction (Fig. 2).

Other cyanobacteria that were also present (*Gomphosphaeria naegeliana* (Unger) Lemm., *Oscillatoria agardhii* var. *isothrix* Skuja, *Oscillatoria.* sp. and *Anabaena* sp.) remained uncolonized.

Variation in vorticellid infestation of colonies

Direct observations made on samples collected from the surface waterbloom in Mitchell Wyke, revealed that there were many fewer vorticellids on the *Anabaena* colonies and some of the colonies were almost devoid of them (Fig. 3). The reason for this remains unknown. Under conditions of stress vorticellids can transform themselves directly into free-swimming telotrochs by the development of a ring of aboral cilia (Fig. 7). They are thus released from attachment to the substrate but their stalks are left behind (Fig. 10). Such telotrochs were present in these samples and possibly were indicative of inimical conditions existing in the dense surface bloom. During swimming, the part of the vorticellid body (scopular region) previously adjacent to the stalk is now directed forwards. In time it is this end that will renew the contact with an *Anabaena* filament (Fig. 8) and later start to grow its stalk (Fig. 9).

Grazing by carnivorous ciliates (see later) may also have had an effect on the numbers of vorticellids present.

Other associated organisms

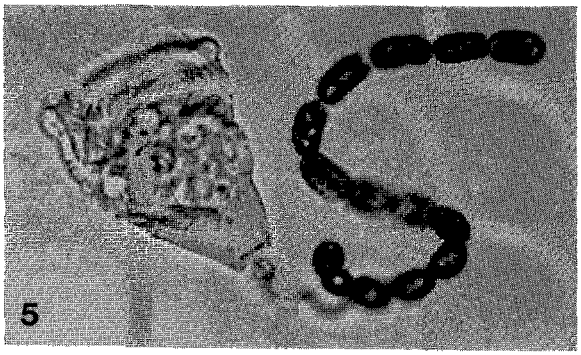
The ciliate *Nassula aurea* Ehrenberg (Canter, Heaney & Lund, 1990) grazed the cells of *A. lemmermannii* (Fig. 4). Samples collected from the surface bloom additionally contained two carnivorous ciliates that fed upon the vorticellids. One was the large *Trachelius ovum* Ehrenberg (Fig. 12), which ingested vorticellid bodies whole. The other was a much smaller unidentified prostomatid ciliate, possibly *Acaryophrya* sp. (Fig. 13), which fed upon individuals by extracting their cell contents.

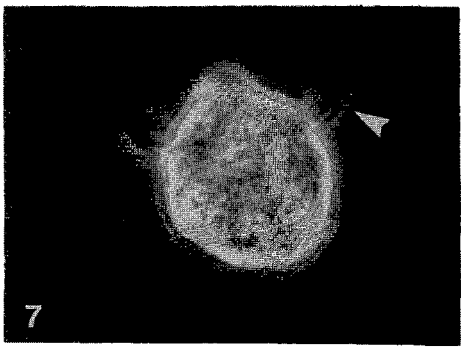
A very few vorticellids were observed that contained what appeared to be a parasite. When young it took the form of a round sporangium 15–19 μm beset with a number of refractive globules (Figs 14–16). Only one mature zoosporangium (22 μm) was seen and it was located free in the medium (Fig. 16). How it became evicted from the vorticellid is not known. Many zoospores were present surrounding what appeared to be a central core of residual material (Fig. 17). The zoospores, 5·4 μm long × 2·5 μm broad (Fig. 18) contained one or two contractile vacuoles and a single flagellum 7 μm long with an additional whiplash ending. Their method of swimming was not observed. More information is needed to resolve the taxonomic position of this organism. It differs from the parasites of vorticellids that have already been recorded, e.g. the fungus depicted by Stein (1859) in *Vorticella* cysts (mistakenly described as part of the protozoan life cycle); *Sporomonas infusorium* Chatton & Lwoff (1924) parasitic in a marine *Vorticella* sp.; and *Meria harposporioides* Barron & Szijarto (1982) in *Vorticella* sp.

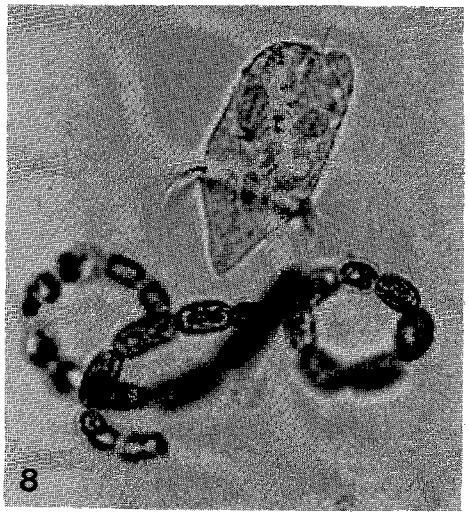
Swimming and floating movements

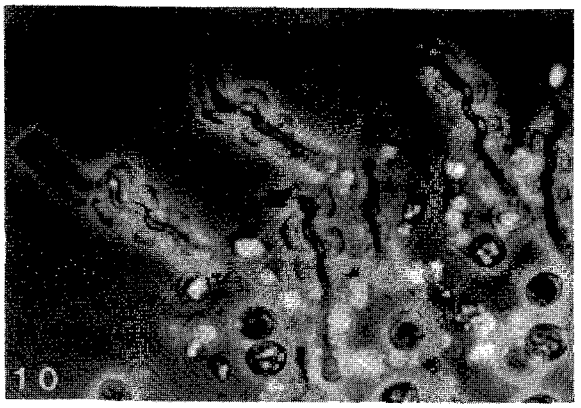
When the colonies from the net tow in the South Basin of Windermere were observed by microscopy in 1 mm deep chambers it was observed that many of those with peritrichs attached showed active rotational or translational movements, evidently propelled by the action of the vorticellids' cilia. Some individual colonies were observed to complete a rotation in 4 to 13 seconds. Many of the "swimming" colonies moved in an erratic fashion without making much headway in any direction while others produced sustained translation. Of these, 14 were timed to cross the space between two graticule rulings 730 μm apart in times of 3–8 s, and showed a mean swimming velocity of 138 μm s^{-1}.

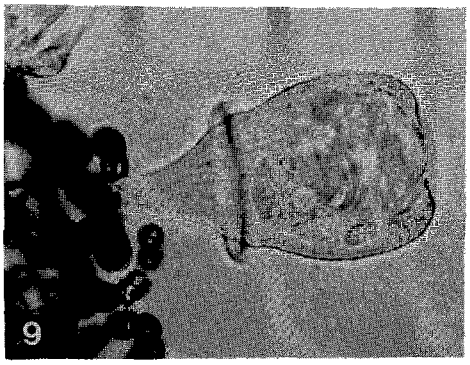
When 5 ml samples of the same net tow were left to stand in a test tube the majority of the colonies soon aggregated at the water surface. In theory this aggregation might have been due either to "swimming" activity (perhaps oriented towards the surface by positive aerotaxis or negative gravitaxis) or



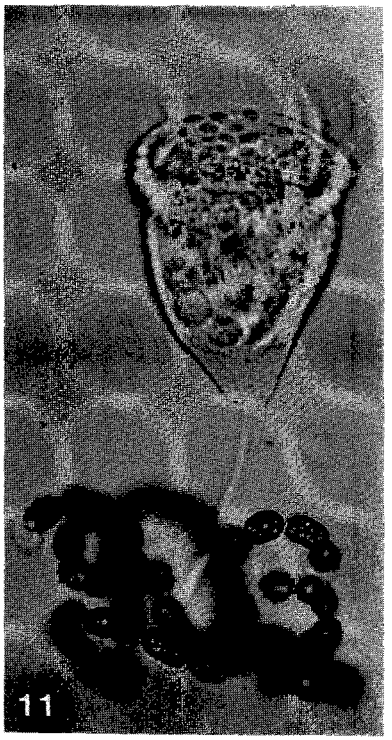


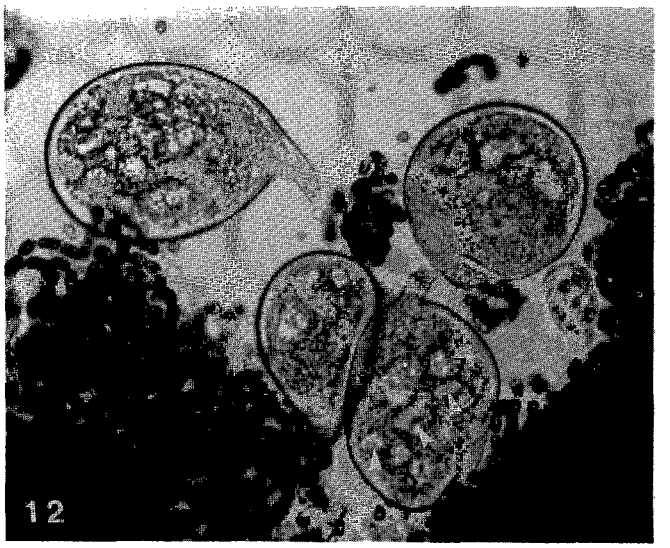


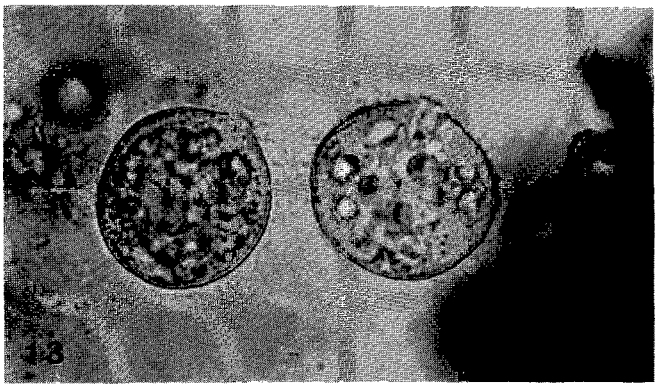


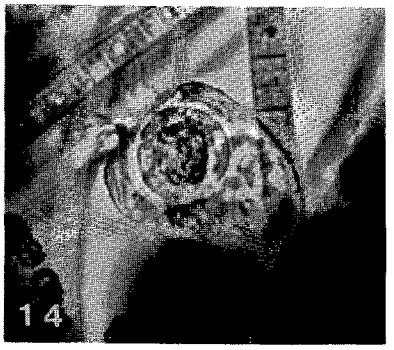


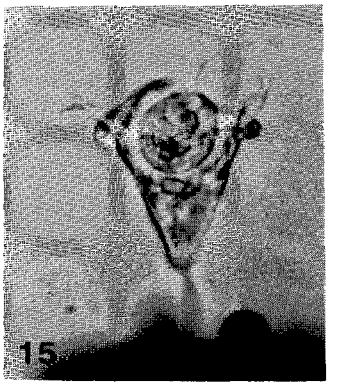
FIGS 5–10. Vorticellids and *Anabaena lemmermannii*. Fig. 5. Vorticellid attached to a short 14-celled filament from a fragmented colony. × 640. Fig. 6. As Fig. 5 but in Indian ink to show mucilage sheath around cyanobacterial cells. × 640. Fig. 7. Free swimming telotroch bearing wreath of aboral cilia (arrowed); direction of motion north. × 640 (phase-contrast). Fig. 8. Telotroch making contact with a filament. × 640. Fig. 9. Settled telotroch, on filament mass, with growing stalk. × 640. Fig. 10. Part of an akinete-bearing *Anabaena* colony (heterocysts alone present in the photograph) with stalks that remain attached to a colony after the direct transformation of a vorticellid into a telotroch or after its death. × 640 (phase-contrast).

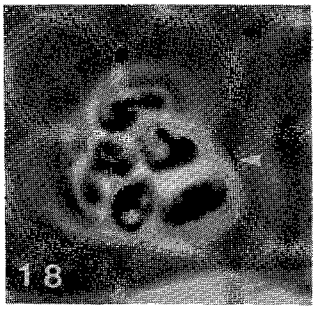

11

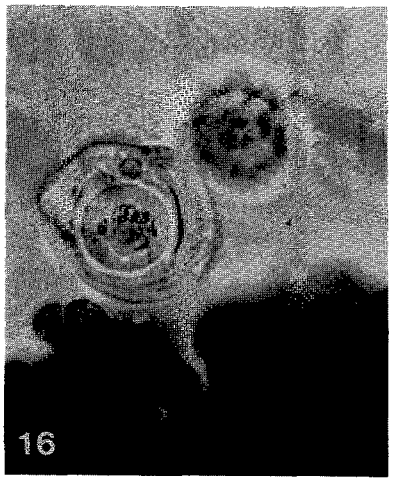

12

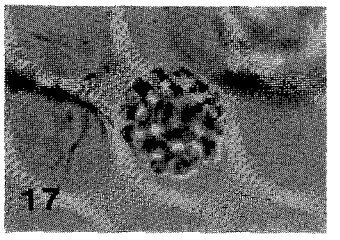

13

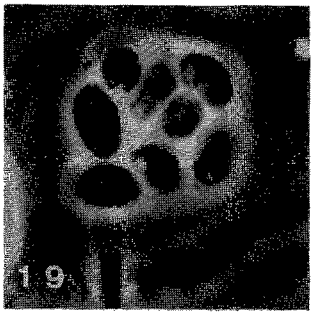

14


15


18


16


17


19

to flotation owing to buoyancy provided by gas vacuoles in the cyanobacteria. The sample was placed in the stout glass tube of a pressure nephelometer (Walsby, 1973) and subjected to a pressure in the overlying gas phase of 1·2 MPa, sufficient to collapse the gas vacuoles (but not to kill the peritrichs or to affect their swimming activity). All of the colonies were observed to sink within 1 min; this clearly established that the upward movement of the suspended colonies was caused by their buoyancy rather than by the swimming action of the attached peritrichs. The buoyancy of the colonies and their floating velocity was investigated in more detail.

In the 1 mm deep counting chambers the majority of colonies were observed in the focal plane just under the coverslip. This was true not only of the stationary colonies but also of the colonies that were rotated or moved along by the "swimming" movements of the vorticellids. The average floating velocity of the buoyant *Anabaena* colonies was 144 μm s^{-1} (Walsby *et al.*, 1991), approximately the same as the average swimming velocity. After collapsing the gas vesicles by application of pressure all the colonies were observed to be in the focal plane just above the slide surface.

Buoyant density of the vorticellids

From these initial observations it was clear that excess buoyancy provided by gas vesicles was sufficient to compensate for the ballast weight of these epizooids in addition to the ballast mass of heavy components of the cyanobacterial cells. An attempt was made to provide a quantitative description of this phenomenon.

It was found that vigorous shaking of a colony suspension for 1 min caused some disruption of the colonies and some of the vorticellids were dislodged. When the shaken suspension was left to stand for a few minutes the fragments of *Anabaena* colonies floated up leaving a partially clarified subnatant containing many vorticellids. Some of them continued to beat their cilia, demonstrating their viability. 10 ml portions of the subnatant were centrifuged at 2000 rpm for 4 min and the pellet, which contained the sedimented vorticellids, was re-suspended in about 0·5 ml of water, layered over a Percoll concentration gradient, and then centrifuged for 4 min at 4000 rpm. No bands were evident but the gradient was separated into fractions that were inspected by microscopy, and the highest concentration of vorticellids was found in a fraction whose buoyant density was measured as 1033 kg m^{-3} see Table I, experiment 1). Some of the vorticellids in this layer also continued to beat their cilia. The experiment was repeated with another suspension of colonies and the separated vorticellids were centrifuged on a

TABLE 1. Buoyant densities of vorticellids separated on Percoll concentration gradients

Experiment	Percoll layer	Vorticellids per field	Density of layer (kg m^{-3})
1	3	0·5	n.d.
	4	2·2	n.d.
	5	3·2	1033
	6	2·1	n.d.
	7	1·9	n.d.
	8	1·3	n.d.
2	1	0	1013
	2	0	1021
	3	30	1030
	4	15	1033
	5	5	1035

n.d. = not determined.

FIGS 11–19. Vorticellids on *Anabaena lemmermannii* together with other associated organisms. Fig. 11. *Pseudovorticella molinata*; pellicular granules visible at apical region. ×640. Fig. 12. Four individuals of the ciliate *Trachelius ovum* each containing many vorticellid bodies (arrowed). ×256. Fig. 13. A prostomatid ciliate, ?*Acaryophrya*, which feeds on the contents of vorticellids. ×640. Figs. 14–16. Single round immature sporangium of a parasite inside each vorticellid; in Fig. 16, but out of focus, is a mature sporangium free in the medium. Figs. 14 and 16 ×640; Fig. 15 ×720. Fig. 17. Sporangium, as Fig. 16; many small zoospores and large central sphere of residue now visible. ×640. Figs. 18, 19. Zoospores, showing contractile vacuoles in various stages of development; in Fig. 18 a single flagellum is visible attached to one of the zoospores (arrowed). ×1600 (phase-contrast).

steeper concentration gradient of Percoll, which gave a sharper separation (Table I, experiment 2). From this, the average buoyant density of the vorticellids was estimated at 1031 kg m^{-3}.

The number of vorticellids that can be lifted by an *Anabaena* colony

The volume of a vorticellid has been determined as approximately that of a cone of base 27 μm and height 47 μm: this gives a volume of 8970 μm^3 which can be rounded up to 9000 μm^3 to include the volume of the stalk. The mass of a vorticellid is given by the product of this volume and its buoyant density, 1·031 pg μm^{-3}. The unsupported "ballast mass" in water, of density 0·998 pg μm^{-3}, is 9000 $\mu m^3 \times 0{\cdot}033$ pg μm^{-3} = 297 pg.

The colonies used in the experiment to determine floating and sinking velocities had an average maximum axial dimension of 188 μm and an axial ratio of 0·613, giving a volume of $1{\cdot}3 \times 10^6$ μm^3. The buoyant density of the colonies with intact gas vesicles has been estimated as 974·7 kg m^{-3} (Walsby *et al.*, 1991), which gives an excess density of −23·5 kg m^{-3}. The ballast mass of the colony is therefore $1{\cdot}3 \times 10^6$ $\mu m^3 \times 0{\cdot}0235$ pg μm^{-3} = 30500 pg. Dividing into this value the ballast mass of a single vorticellid gives 103 as the number of vorticellids that the colony will buoy up.

It was noticed in suspensions of colonies that had been fragmented by shaking that there were vorticellids attached to single filaments (see Figs 5 and 11). Short filaments with single vorticellids attached had sunk onto the slide surface of the counting chamber but some longer filaments, each carrying a single vorticellid, floated under the coverslip: the shortest of these contained only 48 cells. It is estimated that the average vegetative cell of *A. lemmermannii*, a cylinder with truncated spherical ends of average width 6·3 μm and overall length 9·5 μm, has a volume of 280 μm^3. The buoyant density of the filaments was 943 kg m^{-3} (Walsby *et al.*, 1991); the ballast mass of a cell in water would therefore have been 280 $\mu m^3 \times$ (0·943 − 0·998) pg μm^{-3} = −15·4 pg. Dividing this value into the ballast mass of a single vorticellid gives 19 as the minimum number of gas-vacuolate cells required to buoy up one of these ciliates.

DISCUSSION

If a filter-feeding micro-organism is freely suspended in a water mass the beating of its cilia will produce resultant swimming movements. Such an organism is able to produce more effective feeding currents if it is anchored to a surface. The feeding apparatus should then be extended out from the surface to minimize the viscous drag on the current by that surface (Fenchel, 1987). The vorticellids we investigated would derive some benefit, for these reasons, in being attached to the *Anabaena* colonies, rather than being freely suspended in the lake water; this benefit will be greater on colonies that show little net movement as a result of the feeding currents of the vorticellids.

A particular advantage of attachment to the *A. lemmermanni* colonies rather than to other phytoplankters is that these cyanobacterial colonies are highly buoyant and they therefore remain in the epilimnion of the lake for longer periods of time, usually circulated within the well-mixed euphotic zone. Through this attachment the vorticellids obtain a long residence time in this water layer and are able to exploit the population of picoplanktonic organisms, which they filter from the water. This benefit of buoyancy provided by the *Anabaena* colonies is lost, of course, if the number of vorticellids that attach causes them to sink. It was initially surprising to see such highly infested colonies still floating, but the quantitative analysis of the buoyant densities and volumes of the cyanobacteria and vorticellids reveals that large numbers of the latter can attach to a colony of *A. lemmermannii* before it sinks. This remarkable buoyancy is derived from an unusually high gas vesicle content present in the *Anabaena* cells (Walsby *et al.*, 1991).

These results are in accordance with the

large numbers of vorticellids seen attached to balls of *A. flos-aquae* in the plankton by Davis (1973) and Pratt & Rosen (1983). The latter workers found 35–50 vorticellids on colonies 400–600 μm diameter while individual filaments had just one or two attached. For the most part the *Nostoc* colonies (which we consider to be *Anabaena*) observed by Kerr (1983) harboured 1–20 vorticellids. However others supported up to and even in excess of 100 vorticellids. The general similarity between the association described by Kerr (1983, Fig. 4) and that seen on *A. lemmermannii* in Windermere was commented upon by Canter, Heaney & Lund (1990). Abundant vorticellids have also been noted (by H.M.C.) attached to *A. lemmermannii* in several other lakes in the English lake district (e.g., Bassenthwaite Lake, Blelham Tarn, Coniston Water, Crummock Water, Derwent Water, Grasmere, Haweswater and Loweswater) as well as in Malham Tarn, Yorkshire. A similar association was observed in Lake Baikal, USSR, in August 1991 by Dr S. I. Heaney (pers. comm.).

The specific attachment of *V.* (*Pseudovorticella*) *molinata* to *A. flos-aquae* was noted by Pratt & Rosen (1983). Canter, Heaney & Lund (1990), however, described the frequent, abundant occurrence of this vorticellid on *A. lemmermannii*, which was also the case in the present study. In view of the apparent specificity of *P. molinata* it would be interesting to know if the above cyanobacteria in fact represent the same taxon.

The stalks of the vorticellids seem to attach directly onto the cells of the *Anabaena*, apparently penetrating any layers of mucilage sheath that may be present. It is possible that specific attachment by telotrochs may require a chemical attractant to locate the cyanobacterium, and the recognition of a particular surface component.

Horikami & Ishii (1981) found that some *Vorticella* species secrete substances that attract telotrochs to settle close by adults on the same substratum. In this way individuals occur together in large numbers (pseudocolonies). Such a phenomenon might explain some of the massive infestations that have been recorded here.

The *Anabaena* may also derive benefits from the presence of the vorticellids. The feeding currents that bring particulate morsels to the vorticellids will also irrigate the cyanobacteria with solutions of dissolved nutrients (Pratt & Rosen, 1983). The respiration of the protozoa might also produce a local enrichment of CO_2, which could help to relieve a limitation in a soft-water lake such as Windermere. In large numbers they may provide a physical barrier around the cyanobacterium and impede predation of its cells by the ciliate *Nassula* (Canter, Heaney & Lund, 1990).

ACKNOWLEDGEMENTS

We thank Dr B. J. Finlay for help with identification and Dr J. W. G. Lund FRS for his comments on the manuscript. This work was supported in part by grants from the Natural Environment Research Council to A.E.W. and the Royal Society to H.M.C.

REFERENCES

BARRON, G. L. & SZIJARTO, E. (1982). A new hyphomycete parasitic on the ciliated protozoans *Vorticella* and *Opercularia*. *Can. J. Bot.*, **60:** 1031–1034.

CALDWELL, D. E. & CALDWELL, S. J. (1978). A *Zoogloea* sp. associated with blooms of *Anabaena flos-aquae*. *Can. J. Microbiol.* **24:** 922–931.

CANTER, H. M. (1973). A guide to fungi occurring on planktonic blue green algae. In *Taxonomy and Biology of Blue-green Algae* (Desikachary, T. V., editor), 145–158. University of Madras.

CANTER, H. M., HEANEY, S. I. & LUND, J. W. G. (1990). The ecological significance of grazing on planktonic populations of cyanobacteria by the ciliate *Nassula*. *New Phytol.*, **114:** 247–263.

CHATTON, E. & LWOFF, A. (1924). Sur un flagellé hypertrophique et palintomique parasite des infusoires marins: *Sporomonas infusorium* (n. gen., n. sp.). *C.R. Soc. Biol. Strasbourg*, **91:** 186–190.

CMIECH, H. A. LEEDALE, G. F. & REYNOLDS, C. S. (1987). Morphological and ultrastructural variability of planktonic cyanophyceae in relation to seasonal periodicity III. *Gomphosphaeria naegeliana*. *Br. phycol. J.*, **22:** 339–343.

DAFT, M. J. & STEWART, W. D. P. (1971). Bacterial pathogens of freshwater blue-green algae. *New Phytol.*, **70:** 819–829.

DAVIS, C. (1973). A seasonal quantitative study of the plankton of Bauline Long Pond, a Newfoundland lake. *Le Naturaliste Canadien*, **100:** 85–105.

DRYDEN, R. C. & WRIGHT, S. J. L. (1987). Predation of cyanobacteria by protozoa. *Can. J. Microbiol.*, **33:** 471–482.

FENCHEL, T. (1987). *Ecology of Protozoa. The Biology of Free-living Phagotrophic Protists.* Springer-Verlag, London.

HORIKAMI, H. & ISHII, K. (1981). Cluster inducing factor secreted by *Vorticella* telotroch. In *Abstracts of the 6th International Congress on Protozoology, Warsaw. Prog. Protozool.*, p. 145.

KAHL, A. (1935). Urtiere oder Protozoa. I: Wimpertiere oder Ciliata (Infusoria). Eine Bearbeitung der freilebenden und ectocommensalen Infusorien der Erde, unter Ausschluss der marinen Tintinnidae. 4. Peritricha und Chonotricha. In *Die Tierwelt Deutschlands*, (Grimpe, G. & Wagler, E., editors), **30:** 651–864.

KERR, S. J. (1983). Colonization of blue-green algae by *Vorticella* (Ciliata: Peritrichida). *Trans. Am. Microsc. Soc.*, **102:** 38–47.

LUND, J. W. G. (1966). In *Marine Biology II. Proceedings of the Second International Interdisciplinary Conference* (Oppenheimer, C. H., editor), 193–197. New York Academy of Sciences, USA.

LUPTON, F. S. & MARSHALL, K. C. (1981). Specific adhesion of bacteria to heterocysts of *Anabaena* spp. and its ecological significance. *Appl. Environm. Microbiol.*, **42:** 1085–1092.

OLIVER, R. L., KINNEAR, A. J. & GANF, G. G. (1981). Measurements of cell density of three freshwater phytoplankters by density gradient centrifugation. *Limnol. Oceanogr.*, **26:** 285–294.

OLIVER, R. L. & WALSBY, A. E. (1988). Buoyancy and suspension of planktonic cyanobacteria. *Meth. Enzymol.*, **167:** 521–527.

PACE, M. L. & ORCUTT, J. D. (1981). The relative importance of protozoans, rotifers and crustaceans in a freshwater zooplankton community. *Limnol. Oceanogr.*, **26:** 822–830.

PAERL, H. W. (1976). Specific associations of the blue-green algae *Anabaena* and *Aphanizomenon* with bacteria in freshwater blooms. *J. Phycol.*, **12:** 431–435.

PAERL, H. W. (1982). Interactions with bacteria. In *The Biology of Cyanobacteria* (Carr, N. G. & Whitton, B. A., editors), 441–61. Blackwell Scientific Publications, Oxford.

PAERL, H. W. (1988). Growth and reproductive strategies of freshwater blue-green algae (cyanobacteria). In *Growth and reproductive strategies of freshwater phytoplankton* (Sandgren, C. D., editor), 261–315. Cambridge University Press, Cambridge.

PAERL, H. W. & KELLER, P. E. (1978). Significance of bacterial-*Anabaena* (cyanophyceae) associations with respect to N_2 fixation in freshwater. *J. Phycol.*, **14:** 254–260.

PANKOW, H. (1986). Über endophytische und epiphytische Algen in bzw. auf der Gallerthülle von *Microcystis*-Kolonien. *Arch. Protistenk.*, **132:** 377–380.

PRATT, J. R. & ROSEN, B. H. (1983). Associations of species of *Vorticella* (*Peritrichida*) and planktonic algae. *Trans. Am. Microsc. Soc.*, **102:** 48–54.

REYNOLDS, C. S. & WALSBY, A. E. (1975). Water-blooms. *Biol. Rev.*, **50:** 437–481.

SEN, B. (1988). The occurrence of colourless flagellates (*Bicosoeca lacustris, Codosiga botrytis* and *Salpingoeca* spp.) and a green alga (*Stylosphaeridium stipitatum*) epiphytic on phytoplankton of Shearwater. *Arch. Hydrobiol. Suppl.*, **79:** 207–225.

STEIN, F. (1859). *Der Organismus der Infusionstiere nach eigenen Forschungen in systematischer Reihenfolge bearbeitet.* I. Engelmann, Leipzig. 206 pp.

WALSBY, A. E. (1973). A portable apparatus for measuring relative gas vacuolation, the strength of gas vacuoles, and turgor pressure in planktonic blue-green algae and bacteria. *Limnol. Oceanogr.*, **18:** 653–658.

WALSBY, A. E., KINSMAN, R., IBELINGS, B. W. & REYNOLDS, C. S. (1991). Highly buoyant colonies of the cyanobacterium *Anabaena lemmermannii* form persistent surface waterblooms. *Arch. Hydrobiol.*, **121:** 261–280.

WARREN, A. (1986). A revision of the genus *Vorticella* (Ciliophora: Peritrichida). *Bull. Brit. Museum (Nat. Hist.) Zoo. ser.*, **50:** 1–57.

WARREN, A. (1987). A revision of the genus *Pseudovorticella* Foissner and Schiffman 1974 (Ciliophora: Peritrichida). *Bull. Brit. Museum (Nat. Hist.) Zoo. ser.*, **52:** 1–12.

(Accepted 28 October 1991)