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Freshwater protozoa: biodiversity and ecological function

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The purpose of this article is to pull together various elements from current knowledge regarding the natural history of free-living protozoa in fresh waters. We define their functional role, set the likely limits of 'biodiversity', and explore how the two may be related. Protozoa are unicellular, phagotrophic organisms, and 16 phyla of protists contain free-living freshwater protozoan species. They are the most important grazers of microbes in aquatic environments and the only grazers of any importance in anoxic habitats. In sediments, ciliates are usually the dominant protozoans. Benthic ciliate biomass accounts for slightly less than 10% of total benthic invertebrate biomass, but ciliate production may equal or even exceed invertebrate production. Freshwater protozoan species are probably ubiquitous, although many may persist locally for long periods in a cryptic state – as 'potential' rather than 'active' biodiversity. As protozoa are among the largest and most complex of micro-organisms, it follows that bacteria and all other smaller, more numerous microbes are also ubiquitous. The number of protozoan species recorded in local surveys (232) is about 10% of the estimated global species richness (2390). The 'seedbank' of protozoan (and microbial) species ensures that local microbial diversity is never so impoverished that it cannot play its full part in ecosystem functions such as carbon fixation and nutrient cycling.

Keywords: Protozoa; freshwater; biodiversity; species-number; ecological function

1. What are Protozoa?

The taxon PROTOZOA is attributed to Georg August Goldfuss, who proposed the term in 1818 to embrace the 'infusoria', some bryozoans, and various other small animal-like creatures; but it was not until the mid-19th century that the term was first used to refer exclusively to single-celled organisms. In the last 150 years, a wealth of new species has been revealed, revisions to the classification of Protozoa have hardly kept pace (e.g. see Hausmann and Hülsmann, 1995), and even the term Protozoa has experienced difficulties in containing the expanding diversity (giving way in recent decades to re-adoption of Haeckel's 'protista', which includes all protozoa, algae and lower fungi). It has always been difficult to define protozoa. Although they are all unicellular organisms with certain animal-like features, the taxon also harbours blood-parasites, digestive tract symbionts, free-living forms such as the 'slipper animalcule' (*Paramecium*), and the foraminifera whose shells account for a good fraction of the weight in the Egyptian pyramids (Haynes, 1981). But if we focus on those Protozoa that are free-living, we find a discrete group – organisms that share the character of phagotrophy. They may also gain nutrition

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through some photosynthetic ability, but all free-living protozoa have a capacity for phagotrophy, and their diversity has arisen as they have evolved to exploit the diversity of microbial food sources living in all permanent and temporary aquatic habitats (Finlay, 1990).

Protozoa are efficient at gathering microbes as food, and they are sufficiently small to have generation times that are similar to those of the food particles on which they feed. They are, in quantitative terms, the most important grazers of microbes in aquatic environments, and they probably control the abundance of bacteria (Fenchel, 1986b; Berninger *et al.*, 1991; Hobbie, 1994; Sherr and Sherr, 1994). The heterotrophic flagellates alone can probably consume all bacterial production in the aquatic environment (Fenchel, 1986b; Berninger *et al.*, 1991).

Many protozoa are microaerobic – they seek out habitats with a low O_2 tension. This brings them into contact with elevated abundances of microbial food, and it facilitates the maintenance of nutritional symbionts such as sulphide-oxidising bacteria (Fenchel and Finlay, 1989) and endosymbiotic algae – both of which benefit from being located in opposing gradients – O_2 and light on the one hand, and CO_2 , H_2S and other reductants on the other (see Finlay, 1997; Finlay *et al.*, 1997). Many micro-aerobic protozoa can be facultative anaerobes (Bernard and Fenchel, 1996; Finlay *et al.*, 1996b), but unlike the ‘true’ anaerobes (see below) their metabolism is fundamentally aerobic.

A variety of free-living protozoa (ciliates, flagellates and amoebae) have evolved into true anaerobes – and for these, O_2 is toxic. They live principally in freshwater and marine sediments, there are many species, but none is ever abundant (Fenchel and Finlay, 1995). Most use H_2 -evolving fermentations for energy generation, and this provides a substrate (and habitat) for anaerobic bacteria such as methanogens – so methane is released from these ciliate ‘consortia’. Most free-living anaerobic ciliates in freshwater sediments harbour endosymbiotic methanogens, and some may have ectosymbiotic sulphate reducers (Fenchel and Ramsing, 1992; Esteban and Finlay, 1994). Protozoa are probably the only phagotrophic organisms capable of living permanently in the absence of O_2 (see Fenchel and Finlay, 1995).

It is not a simple matter to erect even the basic framework of a classification that might embrace the extraordinary variety of protozoa, and it would be unwise to assume that higher order taxonomy of the group is even approaching a steady state. There is no shortage of well-reasoned classifications of the Protozoa, but Corliss (1994) does have the benefit of attempting to be “user friendly”, and the names of many higher taxa do at least resemble those in the older textbooks. According to Corliss, the Kingdom Protozoa consists of “predominantly unicellular, plasmodial, or colonial phagotrophic, colorless protists, wall-less in the trophic state”. Protozoa ingest other micro-organisms as food, and that fundamental characteristic underpins all functions of free-living protozoa in the natural environment – whether the function is of pivotal and global importance (e.g. as dominant grazers in microbial food webs) or creating functional consortia with methanogens and other micro-organisms. The defining character of phagotrophy dictates that our usage of the term Protozoa should include the Kingdom Protozoa as described by Corliss (1994), plus two other taxa traditionally considered to contain ‘protozoa’, and currently allocated to two other Kingdoms – the Archezoa, and the Chromista (the latter are predominantly phototrophic protists, or ‘algae’).

2. Which Protozoa live in fresh waters?

Freshwater protozoa are found in 16 of the 34 protist phyla in the Corliss (1994) classification (Table 1). Some phyla are particularly well represented, including the ciliates (Phylum Ciliophora), chryomonads (Phylum Phaeophyta), choanoflagellates (Phylum Choanozoa), the naked and testate amoebae (Phylum Rhizopoda), and the heliozoans (Phylum Heliozoa). Searching inside these phyla for the phagotrophic species that are found in fresh waters, we encounter some difficulties. Much information is available for the ciliate species that are characteristic of freshwater sediments (e.g. Finlay *et al.*, 1988 and refs therein) and it is clear that these are, with few exceptions, different from those in marine sediments. It is also true that marine planktonic ciliates are generally different from those in the freshwater plankton, although interestingly, the ciliate community in the brackish-water column resembles that in fresh water – at least at the genus level (Fenchel *et al.*, 1995).

But the non-ciliate protozoa are usually much smaller and more difficult to work with, and taxonomic resolution of these has rarely been attempted in ecological investigations. The latter have focused primarily on the plankton, and on obtaining estimates of abundance, growth and grazing rates of the heterotrophic flagellates. Taxonomy has typically been coarse and flexible (e.g. “bodonids”, “*Spumella*-like”, “kathablepharids”, “large heterotrophic flagellates”). However, with several recent studies, of marine and brackish waters in particular, we have seen rapid expansion in the number of well-described flagellate species (e.g. Patterson and Simpson, 1996; Ekeboom *et al.*, 1996; Larsen and Patterson, 1990; Fenchel *et al.*, 1995; Patterson and Larsen, 1991; Vørs, 1992). Most of these flagellate species appear for the most part to be ubiquitous in marine environments: the same species may occur in both sediments and oceanic water (e.g. Fenchel, 1991), and many species have been recorded from fresh waters and the sea (Larsen and Patterson, 1990; Vørs, 1992). Most benthic ciliates in fresh waters make a living only in fresh waters, whereas many smaller freshwater species, notably the heterotrophic flagellates, may also live in marine environments.

With respect to the definition of where in fresh waters different protozoan species typically live, most information is, again, available for the ciliates, and most of this is derived from studies of temperate freshwater lakes that stratify thermally during the summer months (e.g. Finlay, 1981; Finlay *et al.*, 1988). Characteristic communities are found in specific habitats. In the epilimnion, *Strombidium*, *Askenasia*, tintinnids, peritrichs, small scuticociliates, *Urotricha* and *Balanion* are typically found. Sediment-dwelling ciliates would include *Loxodes*, *Spirostomum*, *Euplotes*, *Frontonia*, large prostomatids and *Dexiotricha*. Following deoxygenation of the benthos, many of these ciliates migrate to the oxic-anoxic boundary in the metalimnion, leaving the (anoxic) benthos and hypolimnion for population growth by anaerobic species (e.g. *Metopus*, *Plagiopyla*, *Saprodinium*, *Caenomorphia*, *Trimyema*; see Finlay *et al.*, 1988; Guhl *et al.*, 1996).

3. Functional groups and ecological roles

The functional roles of free-living protozoa derive from their small size. The smallest are about 2 μm , most flagellates are smaller than 20 μm , amoebae < 50 μm and ciliates < 200 μm . Exceptionally, amoebae and ciliates may reach 2 mm (e.g. *Pelomyxa*, *Actinosphaerium*, *Stentor*). The small size of protozoa has several implications: most prey items will be other, usually smaller microbes; they can have high growth rates that are often

Table 1. A summary classification of the free-living protozoa commonly found in fresh waters, with notes on some defining characteristics and ecological functions¹

| Phylum | Description | Functional Role in Fresh Waters | †Relative Importance in fresh waters |
|-------------------------|---|--|--------------------------------------|
| Kingdom Archezoa | | | |
| ARCHAMOEBAE | anaerobic amoeba-flagellates without mitochondria (e.g. <i>Mastigamoeba</i> , <i>Pelomyxa</i>); also known as ‘pelobionts’ | non-specific feeders (bacteria, algae, detritus, etc.); relatively common in organically enriched, anoxic sediments | + |
| METAMONADA | anaerobic flagellates without mitochondria; mainly endosymbionts, but includes (free-living) ‘diplomonads’ (e.g. <i>Hexamita</i> , <i>Trepomonas</i>), and <i>Retortamonas</i> | bacteria feeders; relatively common in organically enriched, anoxic sediments | + |
| Kingdom Protozoa | | | |
| PERCOLOZOA | a ‘mixed bag’ of amoeboid forms with a transitory flagellated stage (e.g. <i>Vahlkampfia</i>), non-amoeboid forms with four flagella (e.g. <i>Percolomonas</i>), and anaerobic flagellates with modified mitochondria (hydrogenosomes) (e.g. <i>Psalteriomonas</i>) | all live in sediments and feed mainly on bacteria; <i>Percolomonas</i> is a filter feeder; <i>Psalteriomonas</i> is an anaerobe with methanogenic endosymbionts | + |
| PARABASALA | anaerobic flagellates with modified mitochondria (hydrogenosomes); all are endosymbiotic, with the probable exception of <i>Pseudotrichomonas</i> and <i>Ditrichomonas</i> | free-living species probably feed on bacteria; very little known | ? |
| EUGLENOZOA | flagellates, usually with two flagella; those associated with surfaces typically have one trailing flagellum in contact with the substrate, the other pulling the flagellate forwards; many are phagotrophic (e.g. <i>Astasia</i> , <i>Peranema</i> , <i>Anisonema</i> , <i>Entosiphon</i> , <i>Bodo</i>); includes ‘bodonids’, which are biflagellated ‘kinetoplastids’ | phagotrophic species live mainly in sediments where they often glide over surfaces and graze on attached or suspended bacteria, or, as in the case of the larger euglenids (e.g. <i>Entosiphon</i>), larger particles | + (+) |
| OPALOOZOA | a varied assemblage of small, poorly studied flagellates, mostly biflagellated (e.g. <i>Apusomonas</i> , <i>Heteromita</i> , <i>Cercomonas</i> , <i>Cyathobodo</i> , <i>Kathablepharis</i>); this taxon also includes the endocommensal ‘opalids’ | feed mainly on bacteria, in plankton [‡] (esp. <i>Kathablepharis</i> , which also feeds on small algae), and on sediment surfaces, where they also tend to form pseudopodia for feeding (e.g. <i>Cercomonas</i>) or secrete a stalk for attachment (<i>Cyathobodo</i>) | + + |

| | | | |
|------------|--|--|-------|
| CHOANOZOA | the 'collared' flagellates; small (usually < 10 µm), with a feeding filter forming a collar which surrounds the single anterior flagellum; exclusively phagotrophic (e.g. <i>Monosiga</i> , <i>Sphaeroeca</i>). | relatively abundant and important filter feeders, especially of small suspended bacteria (because of the low porosity collar) in the freshwater plankton | ++(+) |
| DINOZOA | flagellates with two heterodynamic flagella; many species marine; some phagotrophic freshwater species in the genera <i>Katodinium</i> , <i>Peridinium</i> , <i>Gymnodinium</i> and <i>Ceratium</i> | typically in the plankton, where phagotrophic species (e.g. <i>Gymnodinium</i>) are occasionally abundant and are known to feed on algae | + |
| CILIOPHORA | a very large and diverse taxon; with cilia used for both locomotion and filter-feeding; generally larger than flagellates; most are free-living; many are anaerobic, with mitochondria acting as hydrogenosomes; many with photosynthetic endosymbionts (algae, sequestered chloroplasts, non-sulphur purple bacteria); common, normally abundant and often the dominant protozoans in soft sediments (e.g. <i>Loxodes</i> , <i>Spirostomum</i> , <i>Caenomorpha</i> , <i>Aspidisca</i> , <i>Acineta</i> , <i>Nassula</i> , <i>Cyclidium</i> , <i>Vorticella</i> , <i>Frontonia</i> , <i>Paramecium</i> , <i>Prorodon</i> , <i>Lacrymaria</i> , <i>Actinobolina</i>); several orders are composed entirely of endosymbiotic species | broad diversity of feeding types (filter, raptorial, 'diffusion', 'hoover'); the smallest species tend to feed on bacteria-sized particles, and the larger ciliates on the larger unicellular algae, filamentous cyanobacteria, other protozoa, and occasionally rotifers and other microzooplankton; common and often abundant in plankton and (especially) in sediments; probably the most important grazers of other micro-organisms in general, in lake and river sediments. Metalimnetic blooms of mixotrophic species (e.g. <i>Halteria viridis</i>) may be significant sources of primary production; many species harbour pro-and/or eukaryotic symbionts | ++++ |
| RHIZOPODA | non-flagellated amoebae, with pseudopodia that serve for locomotion and feeding; in the 'naked amoebae', pseudopodia are lobose (e.g. <i>Acanthamoeba</i> , <i>Amoeba</i> , <i>Platyamoeba</i> , <i>Vannella</i>), or filiform (e.g. <i>Nuclearia</i> , <i>Vampyrella</i> , <i>Asterocaelum</i>); the 'testate amoebae', have either lobose (e.g. <i>Arcella</i> , <i>Nebela</i>) or filiform (e.g. <i>Euglypha</i> , <i>Trinema</i>) pseudopodia. Amoebae with reticulate pseudopodia (the foraminifers) are almost all marine; the taxon includes many endosymbionts (e.g. <i>Entamoeba</i>) | non-specific feeders on whole algae (diatoms, green algae, unicellular and filamentous cyanobacteria), detritus, bacteria etc.; or penetrating and eating green algae (e.g. <i>Vampyrella</i>). Common in sediments and attached to surfaces in plankton (e.g. 'lake snow'); some testates are planktonic (e.g. <i>Diffugia</i>) but rarely abundant; prey size of testates is limited by shell aperture size | ++ |

Table 1. (Continued)

| Phylum | Description | Functional Role in Fresh Waters | †Relative Importance in fresh waters |
|--|---|---|--------------------------------------|
| HELIOZOA | with stiff pseudopodia (axopodia) radiating from the cell (hence 'sun animalcules'), and used for 'diffusion feeding' (prey cells collide with and are trapped by the 'sticky' axopods); common in fresh water (e.g. <i>Actinophrys</i> , <i>Actinosphaerium</i> , <i>Acanthocystis</i> , <i>Hedriocystis</i> , <i>Raphidiophrys</i>) | 'diffusion' feeders esp. of motile and non-motile prey, e.g. algae, protozoa and rotifers; mainly planktonic; large size variation – some e.g. <i>Actinosphaerium</i> , up to 1 mm; small spp. may account for 90% of sarcodine biomass in plankton | + + |
| Kingdom Chromista | | | |
| Although the Chromista are dominated by phototrophs, they contain species that benefit nutritionally from phagotrophy. Mixotrophy (obtaining food using a combination of phagotrophy and phototrophy) is widespread, and in some cases ecologically important (see Sanders and Porter, 1988). Mixotrophy and phagotrophy in freshwater chromists is especially common in the chrysonomads. | | | |
| BICOSOECAE | small biflagellates; typically in a lorica (<i>Bicosoeca</i>) but may be naked (<i>Cafeteria</i> , <i>Pseudobodo</i>); some species stalked, some colonial; most live in fresh waters; superficially resemble the mixotrophic loricate chrysonomads (e.g. <i>Dinobryon</i> , see Phylum Phaeophyta) | most are planktonic filter-feeders, esp. on bacteria; often attached with a stalk to other planktonic particles; common, and sometimes abundant filter-feeders in the water column, where they feed principally on bacteria, but also on larger particles e.g. euglenids, chytrid zoospores | + + |
| DICTYOCHEAE | small, filter-feeding flagellated phagotrophs ('helio-flagellates' or 'pedinellids'), superficially resembling heliozoa and/or choanoflagellates, with (e.g. <i>Actinomonas</i> , <i>Pteridomonas</i>) or without (e.g. <i>Ciliophrys</i>) a stalk | most are filter feeders of bacteria-sized particles; stalked and usually attached to particles of sediment or detritus | + + |
| PHAEOPHYTA | typically phototrophic heterokont* flagellates; the chloroplast is essentially vestigial (and the cell colourless) in phagotrophic genera (e.g. <i>Paraphysomonas</i> , <i>Spumella</i>). There is a continuum of functional types from principally or exclusively phagotrophic (e.g. <i>Paraphysomonas</i>), through the mixotrophs (e.g. <i>Dinobryon</i> , <i>Uroglena</i>) to those that are predominantly phototrophic (e.g. <i>Synura</i> , <i>Mallomonas</i>). The most important phagotrophic forms in fresh waters are in the Chrysophyceae (hence 'chrysonomads') | probably the most abundant of the heterotrophic flagellates in the plankton (e.g. <i>Paraphysomonas</i> and <i>Spumella</i> -like flagellates) and the most important (filter-feeding) grazers of bacteria-sized microorganisms, but may also ingest larger particles – small algae and other protists; may secrete a stalk for temporary attachment to substrates in sediment or in plankton | + + + + |

| | | | |
|--------------|---|---|---|
| HAPTOMONADA | biflagellated anteriorly, with an additional flagellar appendage (the 'haptonema') involved in capturing microbes (known only for marine species e.g. <i>Chrysochromulina</i>); most are phototrophic; often abundant in marine euphotic zone (e.g. <i>Emiliana</i>); some produce toxins (e.g. <i>Prymnesium</i> ; <i>Chrysochromulina</i>) | scale and importance of phagotrophy by freshwater haptomonads is unknown | ? |
| CRYPTOMONADA | most are yellow-brown phototrophic flagellates with two flagella of similar length (e.g. <i>Cryptomonas</i>); common and often abundant in freshwater plankton; some lack plastids (e.g. <i>Chilomonas</i> , <i>Goniomonas</i>); some evidence that they ingest microbes, but no good evidence that phagotrophy is widespread | Colourless species (e.g. <i>Chilomonas</i>) can be relatively abundant, especially when associated with detritus in sediment, but importance of phagotrophy poorly known | ? |

* a biflagellated cell, one flagellum smooth, the other with mastigonemes (hairs)

† largely based on their quantitative importance as grazers

‡ based on personal observations, and Arndt (1993); Biagini *et al.* (1997); Bird and Kalff (1987, 1989); Canter-Lund and Lund (1995); Carrias *et al.* (1996); Corliss (1994, 1995); Farmer (1993); Fenchel (1986, 1987); Fenchel and Finlay (1995); Finlay *et al.* (1988); Finlay *et al.* (1996c); Karpov, 1997; Kirchhoff and Meyer, 1995; Larsen and Patterson, 1990; Larsen and Sournia, 1991; Laybourn-Parry and Rogerson (1993); Mathes and Arndt (1995); Müller (1989); Müller *et al.* (1991); Patterson and Hedley (1992); Sanders and Porter (1990); Šimek *et al.* (1995, 1997); Simpson *et al.* (1997); Vickerman (1991); Weisse (1997); Zimmermann *et al.* (1996)

‡ with respect to bacteria-feeding in the plankton – this invariably also includes autotrophic picoplankton (= unicellular cyanobacteria)

similar to those of their microbial prey; so they can rapidly achieve immense population sizes, and control the microbial populations they graze. Sarcodines and flagellates are generally smaller than ciliates and more limited in the variety of food particles they can eat. This is especially obvious in the planktonic environment, where ciliates are often the dominant grazers of larger microbes such as cryptomonads, dinoflagellates and diatoms (see Finlay *et al.*, 1988). The relative size of the protozoon to its prey also dictates the most efficient food-capturing mechanism. Where the predator:prey length ratio exceeds 10:1, filter-feeding prevails. Where the ratio is smaller than 10:1, raptorial feeding (seeking out and capturing relatively large, individual food particles) is more common (Fenchel, 1986a). Protozoan grazing on microbes also appears to stimulate the whole microbial community – possibly by increasing the rate of turnover of essential nutrients that would otherwise remain ‘locked up’ in bacterial biomass (e.g. Fenchel and Harrison (1976); Rogerson and Berger (1983); Biagini *et al.*, 1998). Thus, grazing by protozoa stimulates the rate of decomposition of organic matter.

There is a close link between protozoan morphology (especially of the food-capturing organelles) and the way in which the protozoon functions as a grazer. So when we divide the free-living protozoa into broad morphological groups, we also divide them into broad functional groups. The three broadest groups would then be: ciliates, sarcodines and heterotrophic flagellates. All three may feed on the same type of bacteria in the same place, but they will differ in the mechanics of food capture (using cilia, pseudopodia and flagella respectively). They also differ in their life styles, morphology, and in the food size spectrum that each can ingest – the amoeba for example will typically engulf a much broader size range than a filter-feeding ciliate of the same size – the ciliate being adapted for filtering a narrow size range of particles.

The functional role of protozoa as phagotrophs is fairly well defined, but it may also be noted that it is difficult to find protozoa that do not have other microbes living inside them or on their external surfaces (see e.g. Esteban *et al.*, 1993b; Fenchel and Finlay, 1989; Fenchel and Ramsing, 1992; Finlay *et al.*, 1991; Finlay and Fenchel, 1992; Fenchel and Finlay, 1995; Finlay *et al.*, 1996b). The real diversity of symbiotic associations involving protozoa is poorly studied, as is the ecological significance of symbioses involving free-living protozoa (e.g. methane generation; intracellular sites for photosynthesis). In many cases the symbionts appear to dictate the ecological function of the protozoan consortium (e.g. Fenchel and Finlay, 1989; Finlay *et al.*, 1996b) and it is of course the phenotype of the protozoan consortium on which natural selection operates.

4. Broad functional groups of free-living protozoa

1. *Ciliates* – there are many species in all size classes from $< 20 \mu\text{m}$ to about 2 mm. They graze bacteria, unicellular algae, filamentous cyanobacteria, other protozoa and occasionally rotifers and microzooplankton – either suspended or attached to surfaces; often numerically abundant and probably the most important protozoan grazers in sediments. There are three sub-groups:- (a) Raptorial feeders catch relatively large food items individually, e.g. diatoms, dinoflagellates, other protozoans, filamentous cyanobacteria; many have a simple apical mouth (e.g. *Prorodon*, *Loxodes*, *Askenasia*); some (e.g. *Lacrymaria*, *Monodinium*, *Dileptus*) may kill motile prey; others (e.g. *Nassula*, *Chilodonella*) ‘hoover’ diatoms and other food particles. Some filter-feeders (e.g. *Frontonia*, *Disematostoma*) have a supplementary raptorial capability to feed on relatively large food particles (e.g.

dinoflagellates and filamentous cyanobacteria). (b) True filter feeders use a filter to remove microbial food from suspension; some (e.g. *Cyclidium*) have a relatively large, fine-mesh filter – used for catching suspended bacteria. These ciliates are usually small ($\sim 25 \mu\text{m}$) and relatively abundant in sediments. The filter is much reduced in ciliates (e.g. *Colpidium* and *Glaucoma*) that feed in patches of high bacterial concentrations, and the filter is expansive, and encircles the apical end of the ciliate in the peritrichs (e.g. *Vorticella*), most of which are raised on stalks. In many ciliates (e.g. *Oxytricha*, *Spirostomum*, *Hypotrichidium*, *Aspidisca*) a dense row of membranelles generates a water current and collects the food particles carried in it, which are usually relatively large (e.g. microalgae). Some of these generate more effective feeding currents by raising the cell on ‘walking’ cirri (e.g. *Euplotes*, *Stylonychia*) or by creating a stalk-like extension of the body, aligned perpendicular to the substrate (e.g. *Stentor*); others are typically planktonic (e.g. *Halteria*, *Tintinnopsis*, *Strombidium*). (c) Diffusion feeders (e.g. *Podophrya* and other Suctorina) – swimming prey (usually other protozoa) collide with their sticky tentacles, through which the prey contents are then ‘sucked’; they are common in sediments but rarely abundant.

Anaerobic species have evolved in all three ciliate functional groups, including the suctorians (e.g. *Sphaerophrya*).

2. *Sarcodines* – these can be divided into the three broad functional groups of: naked amoebae, testate amoebae and heliozoans. All engulf their prey with pseudopodia, even if it is first necessary to break through the cell wall of the prey (as performed by *Vampyrella*, see Canter-Lund and Lund, 1995), or after capture on axopodia (as in heliozoans). The prey are principally bacteria or algae, depending on the size of the sarcodine grazer, but a great variety of non-living organic particles and aggregates are also often ingested (e.g. by *Pelomyxa*). The majority of sarcodines apart from the heliozoans (which are the only truly planktonic group) are usually associated with surfaces, and especially sediments. Amoebae are uniquely able to persist in very thin water films. The testate amoebae are, because of their resistance to desiccation, probably more important in soils than in lake sediments.

3. *Heterotrophic Flagellates* – the flagella are used for locomotion, feeding, or both. Flagellates are the principal consumers of suspended bacteria, and important grazers of the bacteria associated with surfaces and sediments. Those feeding on suspended particles may feed by direct interception (also known as raptorial feeding) (e.g. the chrysomonads), by filter-feeding (e.g. the choanoflagellates), or by ‘diffusion’ feeding (e.g. *Ciliophrys*). Filter-feeders have relatively large filter areas and the highest volume-specific clearance values – hence competitive superiority over filter-feeding ciliates. It is possible that most suspension-feeding flagellates which create water currents are usually attached to substrates, including suspended particle aggregates and larger planktonic organisms. Fenchel (1991) has observed that this behaviour is not shared by phototrophic flagellates and that attachment may therefore increase the effectiveness of particle uptake by the heterotrophic species. Osmotrophy in flagellates is probably of no quantitative importance, as the much smaller heterotrophic bacteria will always have a competitive advantage.

Note that the functional groups described above are poorly correlated with the foregoing taxonomic groups. Different species may have very similar ecological functions, but be placed in quite different taxonomic groups. Thus heliozoans and helioflagellates lie in different phyla, but they are morphologically similar, and with respect to food particle capture, they function in similar ways. The same could also be said for the cercozoan Opalozoa and the naked amoebae (Rhizopoda), or the bicosoecids and the chrysomonads.

5. Relative importance of protozoa

There is now general agreement that grazing by protozoa is quantitatively important: flagellates and the smaller ciliates are the major consumers of picoplankton (bacteria and the smallest cyanobacteria) in freshwater lakes (see Šimek *et al.*, 1997). Amongst the heterotrophic flagellates, small, bacterivorous forms are usually numerically dominant. Most belong to one of three broad taxonomic groups – the chrysomonads (especially *Paraphysomonas* and “*Spumella*-like” forms), bodonids and choanoflagellates. In a study of a eutrophic reservoir, Šimek *et al.* (1997) showed that these flagellates consumed about 80% of bacterial production in the water, while the remainder was grazed by ciliates. And with calculated doubling times of approximately one day, it is clear that such protozoa can control bacterial production in the water column. This conclusion is supported by a vast amount of published information, mainly from temperate lakes (e.g. Berninger *et al.*, 1991, 1993; Mathes and Arndt, 1995; Weisse, 1997; and see refs in Šimek, *et al.*, 1997).

The other heterotrophic flagellates in the water column are typically less abundant and probably not true ‘bacterivores’ (e.g. *Cercomonas*, *Goniomonas*, and the enigmatic *Streptomonas* [Patterson and Zölffel, 1991]). The only other group that is periodically abundant are the raptorial Kathablepharids, often seen ingesting unicellular cyanobacteria in the size range 1–4 μm (e.g. Weisse, 1997).

The relative importance of different protozoan groups in the plankton varies with the available food resources, and thus with lake and season. In Lake Neumühler (Mathes and Arndt, 1995), ciliates dominated the biomass in late spring, summer and autumn, the smaller flagellates were important in late summer and in winter, whereas the larger flagellates dominated in early spring. Ciliates (mainly oligotrichs, peritrichs, prostomatids and heterotrichs) accounted for 50% of protozoan biomass, small heterotrophic flagellates (chrysomonads, kathablepharids and choanoflagellates) for 29%, large heterotrophic flagellates (dinoflagellates and chrysomonads) for 19%, and sarcodines (heliozoans, testates and naked amoebae) for 2%.

The relatively low sarcodine contribution to planktonic biomass and grazing is typical (Arndt, 1993), although they may occasionally be important (Arndt, 1993; Canter and Lund, 1968). Most planktonic naked amoebae are probably associated with particles – a phenomenon that is better documented for marine environments (e.g. Rogerson and Laybourn-Parry, 1992) than for so-called ‘lake snow’ (see Grossart and Simon, 1993). Suspended particles and aggregates may be sites of elevated abundance of stalked heterotrophic flagellates: Carrias *et al.* (1996) concluded that “attached bacterivores” accounted for 66% of bacterivory by protozoa in the plankton.

A common observation in productive lakes is that extremely dense ciliate populations often develop in the steep chemical gradients of the metalimnion (e.g. Finlay *et al.*, 1996b). Many of these ciliates arrive there having been forced out of the sediment by deoxygenation of the bottom water (Finlay, 1981). They then feed on the autotrophic microbial production which thrives in the metalimnion, where dissolved O_2 overlaps the upwards diffusing CO_2 and reductants (Finlay *et al.*, 1988; 1996b; 1997). The ciliate community develops in a tight band, where its biomass may account for >90% of protozoan biomass (Finlay *et al.*, 1988). Most of these ciliates will later return to the sediment, following the collapse of thermal stratification in the water column.

Protozoa can contribute substantially to total zooplankton production in the water column of lakes. In Lake Constance (Weisse, 1997), heterotrophic flagellates and rotifers

each contributed 15% of total zooplankton production; and ciliates contributed up to 32% of the zooplankton biomass in Lake Oglethorpe (Pace and Orcutt, 1981). The contribution from all protozoa must obviously be higher: Mathes and Arndt (1995) calculated that for Lake Neumühler the protozooplankton average contribution to total zooplankton biovolume was 21%, although it ranged from 3% to 78%. In Lake Oglethorpe the protozoan contribution ranged from 15 to 62% (Pace and Orcutt, 1981). The relative protozoan contribution increases as the trophic status increases – thus Mathes and Arndt (1994) showed that protozoa accounted for 20% of total zooplankton biomass in meso-eutrophic lakes, and up to 50–60% in hypereutrophic lakes. This increasing trend continues towards lake sediments, where rotifers and crustacean zooplankton become relatively unimportant. Large as these figures are, they still understate the quantitative significance of protozoa, which have weight-specific metabolic rates (and growth rates) that are much higher than those of metazoans (see Fenchel and Finlay, 1983).

Finally, we should mention the role of protozoa in channeling biomass from the planktonic microbial foodweb to the metazoan zooplankton. Sanders and Porter (1990) showed that *Daphnia ambigua* was able to grow and produce viable young on a diet of heterotrophic flagellates; and a wide range of copepods, cladocerans and rotifers are known to feed on ciliates (Jack and Gilbert, 1997). This is believed to be a quantitatively important trophic link – at least in some seasons, in some lakes (Stoecker and Capuzzo, 1990; Wickham and Gilbert, 1993).

6. Benthos

A cursory investigation with a microscope of the soft sediments of lakes and rivers gives the impression that most of the phagotrophic activity resides in the protozoa. In the more productive sediments, most of the organisms that are seen moving are protozoa, and these are predominantly ciliates. Unfortunately, while there is much quantitative and qualitative information for ciliates in sediments (e.g. Goulder, 1974; Finlay, 1980; Finlay *et al.*, 1979; Sleigh *et al.*, 1992), there is little for the sarcodines and heterotrophic flagellates – mainly because of practical difficulties associated with studying these groups. There are, however, some spectacular exceptions, such as the very large naked amoeba *Pelomyxa* living in the anoxic benthos, which in one example (Finlay *et al.*, 1988), had an estimated biomass equivalent to 23 kg dry weight ha⁻¹.

Benthic freshwater protozoa overlap in their niche requirements with nematodes, rotifers, tardigrades and gastrotrichs. The relative importance of these is not well known although it is likely that protozoa, because of their great abundance (Finlay and Fenchel, 1996), are indeed quantitatively the most important grazers in the benthos. This can be tested by comparing estimates of benthic production (of ciliates) as a proportion of total benthic invertebrate production (Wetzel, 1983) (Table 2).

It is likely that ciliates contribute the great majority of the biomass (e.g. Baldock *et al.*, 1983) and perhaps up to 75% of protozoan production (Sleigh *et al.*, 1992) in most freshwater sediments, apart from the short period following the introduction of a substantial pulse of organic matter, when heterotrophic flagellates quickly become dominant (because of their intrinsically higher growth rates; Fenchel and Finlay, 1983). Taking the ciliate biomass alone, we find that it accounts, on average, for slightly less than 10% of total benthic invertebrate biomass. In contrast, and as a consequence of the substantially higher specific growth rates in protozoa, ciliate production in the benthos may equal or

even exceed that for the invertebrates. The ciliate value may be an overestimate, as it is largely based on data from productive lakes, with the assumption of continuous growth at near-optimal conditions (Finlay, 1978). Nevertheless, it can be reduced by a factor of two and still be equivalent to the average total for all (non-protozoan) benthic invertebrates.

7. Biodiversity

There are signs of movement towards a consensus regarding the likely nature and scope of species richness in free-living protozoa (Fenchel, 1993; Finlay, 1997; Finlay *et al.*, 1996a; 1998), although there is still no universal agreement on what constitutes a protozoan 'species'. The most widely used, most practicable, and best justified species concept is probably the morphospecies. The latter is particularly relevant in protozoa because of the strong link between form and function, the demonstrated evolutionary convergence towards "adaptive peak" morphological phenotypes (Nanney, 1982), and the lack of any correlation between genetic isolation and genetic divergence ('biological' and 'genetic' species respectively; see Finlay *et al.*, 1996c).

The only recent synthesis of the global number of freshwater (morpho)species of protozoa is that prepared for the ciliates (Finlay *et al.*, 1996c). In this work, the number of nominal species is reduced to around 3000. This relatively low number takes account of known rates of synonymy and cosmopolitan distribution of the vast majority of species (this is probably true for all protozoa, as it is for microbes in general; Finlay *et al.*, 1996a; Fenchel *et al.*, 1997).

The relevance of any figure for 'local' species diversity of protozoa depends on the precision with which 'local' is defined. If we take a 1ml sample of water from a freshwater lake, we expect to find up to 15 ciliate species (Finlay and Esteban, 1998), and if we sum up the different species in 1ml taken from a large number of depths in the stratified water

Table 2. Estimates of biomass and annual production (dry weight) of ciliates and total benthic fauna (non-protozoan invertebrates) in lakes and rivers

| | Ciliates | Invertebrates |
|--|----------------------|-----------------------|
| Biomass (kg ha ⁻¹) | | |
| range | 0.2–69 ^a | 1–100 ^d |
| arithmetic mean | 1.5 ^b | 22 ^d |
| Production (kg ha ⁻¹ year ⁻¹) | | |
| range | 50–1700 ^c | 4.5–2000 ^e |
| arithmetic mean | (564) ^c | 290 ^e |

^a total range including a productive lake in Scotland (Finlay, 1978), and a lake with seasonal deoxygenation of the benthos, in England (Finlay, 1982); both studies over two years.

^b using an average benthic ciliate abundance of 75 per 25 µl (see Fig. 1), and an average ciliate biomass of 5 ng dry weight.

^c using only five annual estimates – for each of three sites in a productive lake (Finlay, 1978), Schönborn's (1981) estimate for a small stream, and the chalk stream estimate given by Sleight *et al.* (1992). Madoni (1987) determined ciliate production in a ricefield, over three months, with an annual equivalent figure of 936 kg DW ha⁻¹ year⁻¹.

^d from Wetzel (1983), Table 21-17 – total range and arithmetic mean ($n = 38$)

^e from Wetzel (1983), Table 21-18 – total range and arithmetic mean ($n = 17$)

column of a productive lake, we may find 20–40 species on a single occasion. In the sediment, where ciliates are much more abundant (typically 100–10000 per cm^2 , compared to 1 to 100 per cm^3 in the water column – see Finlay and Fenchel, 1996) a small, manageable sediment sample of 25 μl will contain up to about 30 ciliate species (Fig. 1). And if the same benthic site is examined regularly over a period of two years, 100 species or more will be recorded (Finlay, 1998). Our inventory of ciliate species recorded from a single, one-hectare pond, over a period of several years, currently stands at about 260 species. This number is still increasing and it currently represents almost 20% of all known freshwater ciliates. Note however that if we remove a small sample of sediment from a freshwater lake and manipulate it to produce a variety of niches for a wide range of ciliate species, a previously hidden diversity will appear. Although only about 20 ciliate

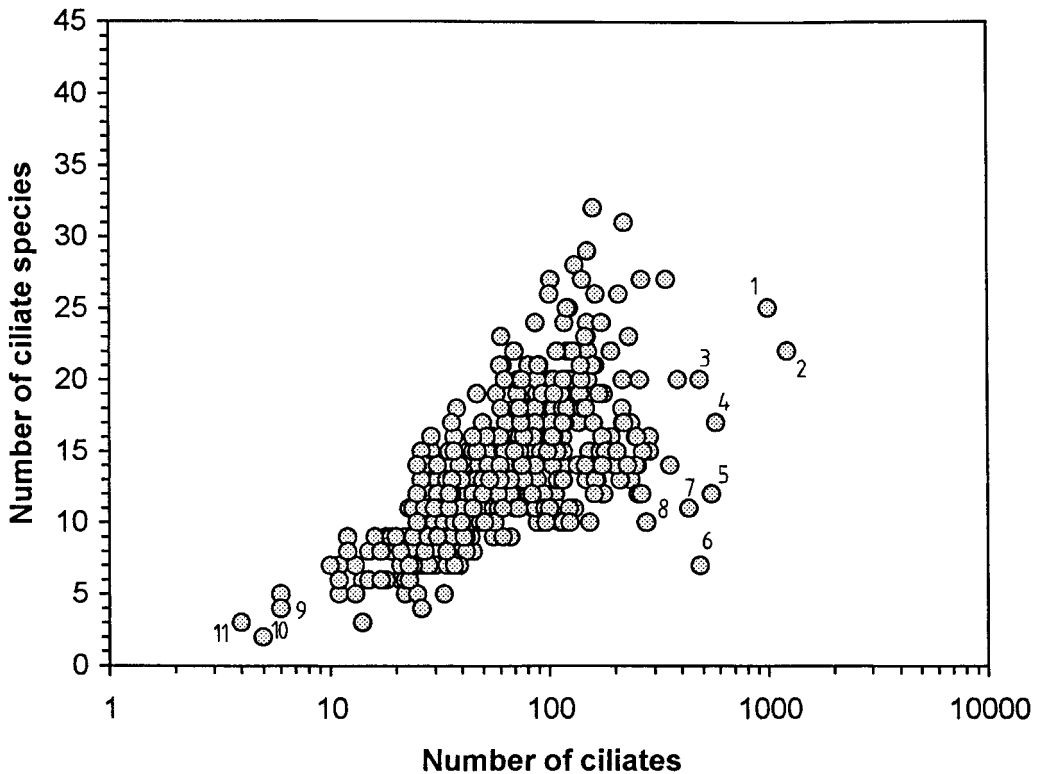


Figure 1. Species richness of free-living ciliates in sediments from freshwater lakes and rivers. The bulk of the data are from productive freshwater lake sediments (Airthrey Loch, Scotland; and Esthwaite Water, England). The remainder are from a variety of lakes spanning the full range of trophic status in the English Lake District, Cumbria, and from river sediments on the Jos Plateau in Nigeria. Each datapoint shows the number of ciliate species and number of ciliates recorded in a sample of approximately 25 μl taken from the top 1 cm of sediment. Numbered datapoints are as follows: 1 and 2 – ciliate communities dominated by massive numbers of a single species (*Dexiotricha* sp.); 3, 4, 5, 6, 7 – from organically polluted streams in Nigeria; 8 – with a water temperature of 37°C at the sediment-water interface; 9, 10, 11 – from sediment at a water depth of 76 m in Wastwater – a large, extremely oligotrophic lake in the English Lake District. ($n = 403$)

species were detectable in the freshly collected sample, 135 species revealed themselves over a three-month period (Finlay *et al.*, 1996a; Fenchel *et al.*, 1997). From a human perspective, a single pond may fit into the category of 'local' scale, but from a protozoan perspective, the pond will provide habitats, both temporary and long-term, for many species. As protozoan species are probably globally ubiquitous, there is every reason to believe that all species of freshwater protozoa could eventually be discovered in one small pond.

It is however quite difficult to define what we mean by 'local'. It may mean a single sample of sediment from a pond, or the species recorded from the water column over a season. It may even refer to an entire river basin. But the curious thing is that the total amount of effort devoted to any study, irrespective of its geographical scope, may be relatively constant and perhaps determined by the time span and financial resources of research grants. As much effort may be devoted to extensive experimental manipulation of a single sediment core as to many individual sediment cores examined over a period of one to two years. In the case of ciliates, in both cases we arrive at 100–150 species. 'Local' means nothing more than what is usually discovered in a small area within the lifetime of an average research project, conducted by people who know what they are doing. 'Global', then, is the aggregate of the historical record from all scientific investigations in all parts of the world (Table 3).

8. Protozoan diversity and ecosystem function

There is much evidence to indicate that each protozoan species thrives best wherever it finds a specific combination of environmental conditions, that the same species will be found wherever this combination occurs worldwide, and that protozoan species appear therefore to be cosmopolitan in their spatial distributions (see Finlay, 1997). The fundamental reason for this (Fenchel, 1993) is that each species is represented by an extremely large number of individuals, and for purely statistical reasons, these individuals are continually being dispersed on a global scale – i.e. they are ubiquitous. In many places, an individual species will be represented by only a few individuals, or perhaps as cysts, but when appropriate conditions are provided, that species flourishes and becomes abundant. Protozoa are amongst the largest and most complex of micro-organisms, so it is likely that if protozoa are ubiquitous, bacteria and all other smaller, more numerous microbes are also ubiquitous.

The ubiquity of microbial species is pertinent to any discussion of the relationship between microbial diversity and ecosystem function. Finlay *et al.* (1997) have shown how the nature and scale of many aquatic ecosystem functions, such as carbon-fixation in a freshwater pond, appear to be driven by complex reciprocal interactions involving physical and chemical factors, and the activities of the microbes themselves. These interactions continuously create new microbial niches, and these are quickly filled from the locally available diversity of rare and dormant microbes (Finlay *et al.*, 1996c, Fenchel *et al.*, 1997), to create new reciprocal interactions between microbes and the physical-chemical environment. If recently-created microbial niches are quickly filled, the number of microbial species that are active at any point in time will be identical to the number of microbial niches currently available, which as we have seen, depends upon the interaction between microbial activity and the physical-chemical environment. So we might define microbial (bio)diversity at any moment as the number of filled microbial niches. Microbes

Table 3. Local and global species richness of free-living protozoa in freshwater environments

| | Local | Global |
|---------------------------|------------------|-------------------|
| Ciliates | 127 ^a | 1500 ^b |
| Sarcodines | 70 | 540 |
| Naked amoebae | 30 ^c | 220 ^d |
| Heliozoans | 15 ^e | 120 ^f |
| Testate amoebae | 25 ^g | 200 ^h |
| Heterotrophic flagellates | 35 ⁱ | 350 ^j |
| Total | 232 | 2390 |
| Local/Global | ~10% | |

^a There is no shortage of published ciliate data, and these fall into two broad categories. In the first, are those pertaining to a single water or substrate sample taken from one place or depth, or even an integrated sample representing a depth range in the water column on a single occasion. It is sometimes difficult to discover how large the samples were, and if they consisted of water, substrate, or a mixture of both. This is especially so in the case of samples taken from rivers. In the second category are those studies that combine data for one site e.g. those from a small pond on many occasions, perhaps over several years, or combined data from a river basin, or a group of lakes and ponds in a small geographical area. This category does *not* include any of the published studies purporting to provide species lists for the areas enclosed by national boundaries (e.g. Bhatia, 1936). No clear distinction can be drawn between the two categories, and indeed their ranges overlap. We may refer to these datasets as 'single' and 'multiple' respectively, with ranges 2–65 and 30–300 species, and 'best estimates' for representative values, of 20 and 200 species respectively. The 'local' figure given is simply the arithmetic mean of all 18 values appearing in the 'multiple' list below. The data included in the 'single' range (and based on samples of various sizes) were taken from the following:- 1. Bamforth *et al.*, 1987 (L. Victoria weed littoral, 32 spp.; L. Naivasha weed littoral, 24 spp.). 2. Beaver and Crisman, 1989 (water column of 30 Florida lakes differing in trophic status; 18 spp. [range 8-27]). 3. Cairns and Ruthven, 1972 (surface waters Abaco Island, Bahamas; 6 spp. [range 2-9]). 4. Esteban *et al.*, 1993a (anoxic hypolimnion, solution lake, Spain; 14 spp.). 5. Finlay *et al.*, 1987 (soda lake [L. Simbi, Kenya] whole water column; 5 spp.). 6. Finlay *et al.*, 1987 (L. Nakuru [Kenya] littoral; 27 spp.). 7. Finlay *et al.*, 1988, Finlay and Esteban, 1998 (water column of Priest Pot [pond]; 6–37 spp.). 8. Finlay and Esteban, this article (403 sediment samples from lakes and rivers differing in trophic status – see Fig. 1; 14 spp. [range 2-32]). 9. Finlay *et al.*, 1993 (1 m² river sediment, Spain; 65 spp.). 10. Foissner *et al.*, 1992 (River Amper, Germany; several substrate types at each station combined on each occasion; 54 spp. [range 38-77]). 11. Müller *et al.*, 1991 (L. Constance, top 8m, single occasion; 16 spp.). 12. It may also be noted that Fenchel *et al.* (1995) recorded 37 ciliate species from the entire water column of a brackish water fjord (Denmark), on a single occasion. The data included in the 'multiple' range were taken from the following:- 1. Bryant and Laybourn, 1972/73 (L. Leven, 11 months, UK; 59 spp.). 2. Cairns, 1965 (Conestoga River basin, Penn. USA; 142 spp.). 3. Cairns, 1966a (Potomac River sediment, USA, over several years; 269 spp.). 4. Cairns and Yongue, 1966 (Douglas Lake region, USA; 101 spp.). 5. Cairns and Dickson, 1972 (South River, Virginia, USA; 81 spp.). 6. Finlay *et al.*, 1988, Finlay and Esteban, 1998 (Priest Pot [one hectare pond, UK]; 56 spp. [two occasions, several places in pond]; 244 spp. [total ciliate inventory for pond]). 7. Finlay *et al.*, 1996a (Esthwaite Water, UK, two years; 104 spp.). 8. Foissner, 1980 (77 small water bodies, Austrian Alps; 194–300 spp. "at a rough estimation 300 species occur frequently in the investigated area"). 9. Grabacka, 1971 (three ponds, Poland; 62 spp.). 10. Gray, 1952 ("current core" of a chalk stream, UK; 36 spp.). 11. Müller *et al.*, 1991 (L. Constance, top 8m over 3 years; 30 spp.). 12. Noland, 1925 (80 collections over two years; 65 spp.). 13. J.L. Olmo, pers. comm. (Guadarrama River basin, Spain; 192 spp.). 14. Small, 1973 (polluted stream, Illinois, USA; 155 spp.). 15. Wang, 1928 (surface water of pond, over one year; 109 spp.). 16. Webb, 1961 (lake sediment, Esthwaite Water, UK, two years; 93 spp.).

^bThis number was obtained using the following assumptions. The non-marine total of 2152 species obtained from taxonomic analysis (Finlay *et al.*, 1998) was reduced by excluding those ciliates recorded only from soil. This gives a 'taxonomic estimate' of 2049 free-living ciliates recorded from the freshwater benthos and plankton of lakes and rivers, bogs and (fresh) ground waters. A recent comparison of independent methods of estimating the number of ciliate species in the freshwater benthos (extrapolation from ecological datasets, and taxonomic analysis) indicates that the average estimate from the two methods has a value that is 77% of the 'taxonomic analysis' estimate (Finlay, 1998; Finlay *et al.*, 1998). Assuming that a 'best estimate' for the number of *all* free-living freshwater ciliates can be produced in the same manner, we arrive at a figure of 1578 species. As it is likely that the number of free-living ciliates will be reduced in future in response to taxonomic revisions of some crowded genera (Finlay *et al.*, 1996a) and the elimination of synonyms, a round figure for the best estimate is 1500.

^cDerived from Wang (1928), O'dell (1979), Finlay *et al.* (1988), Smirnov and Goodkov (1996) (the total of 39 species recorded during this 4-year study of the freshwater sediments of a lake in Karelia, does not include representatives of the Vahlkampfiidae), and Anderson (1997). The upper end of the range (currently 6–45 spp.) would probably be extended if more information was available for the filose and granuloreticulose amoebae.

^dPage's (1988) "gymnamoebae" – i.e. the "naked, non-sporulating, lobose amoebae", which includes all freshwater and terrestrial representatives of the Vahlkampfiidae, the genus *Pelomyxa*, and the Class Lobosea. A global range estimate (111–211 species) can be drawn from this work. The lower end of the range is the total number of 'good' species described by Page. The higher figure includes species of uncertain taxonomic status or those that are unrecognisable on the basis of incomplete published descriptions (according to Page). It also includes the naked freshwater species of filose (e.g. *Nuclearia*) and the granuloreticulose amoebae described in Page and Siemansma (1991). The number of described marine gymnamoebae species is similar to the number described from soil and freshwater i.e. 100–200 species; see Page (1983). This is consistent with Schaeffer's (1926) view, formed after he removed many synonyms and doubtful species, that the total number of "good" marine and freshwater species was around 200. It is likely, however that a good number of very small species of naked amoebae have not yet been discovered (see Rogerson and Laybourn-Parry, 1992; Butler and Rogerson, 1995), for which some allowance is given in the global estimate shown here.

^efrom Nicholls (1983) (13 *Acanthocycytis* species recorded from Ontario lakes and ponds; 1–5 spp. per water body); Wailes (1939) found 6 spp. in 60 preserved net samples obtained over a 15-month period; Wesenberg-Lund (1904) – two species in plankton of four Danish Lakes. Zimmermann *et al.* (1996) identified representatives of seven genera from the water column of Lake Constance. Rainer (1968) found up to 19 species living in the surface sediment of a lake on a single occasion. Webb (1961) found 7 spp. in the sediment of Esthwaite Water (UK). Wang (1928) found 5 species in a pond in Philadelphia (USA), and Finlay *et al.* (1988), two heliozoan species on one occasion in Priest Pot (UK).

^fPage and Siemansma (1991) list 102 spp. of heliozoans from fresh waters. This includes actinophryids, ciliophryids, desmothoracids, centrohelids, dimorphids, and those heliozoans placed within the filose amoebae (Filosea) (e.g. *Rabdiophrys*). This is still a relatively poorly-studied group – hence the slightly increased global estimate shown.

^gThere is a vast literature on this. Examining a sample of 19 papers published over the last 40 years, the 'local' number of testate species is in the range 1–134, with a mean figure of 20. The upper figure is for a freshwater catchment in northern Sweden (Schönborn, 1966), with totals for individual habitats ranging from 4–48. Thomas (1955) recorded 1–16 species in different parts of a pond, and 35 species in the whole pond. Green (1966) found 17 and 27 species in two freshwater ponds in

Malaysia; and Decloitre (1958) – 16 and 35 species in two small ponds next to a river in Cameroun. Green (1963) recorded 5–20 species in the water column of the River Sokoto (Nigeria), the highest numbers when the river was in flood; and Jax (1997) identified 18 and 20 species on glass slides retrieved from the aufwuchs at two sites in a small river (Ilm, Thuringia, Germany). Webb (1961) found 12 species of testates in the sediment of Esthwaite Water (UK). Wang (1928) found 14 in a pond in Philadelphia; Finlay *et al.* (1988), 24 species on one occasion in Priest Pot (UK).

^h This is a guess. Ogden and Hedley (1980) recognised “more than 150 species recorded from the British Isles”. As most, if not all species appear to have cosmopolitan distributions, a global estimate of 200 species may be realistic.

ⁱ There are insufficient data to provide a sound figure. The original data used were:- 1. Cairns, 1965 (Conestoga River basin; 61 spp.); 2. Cairns, 1966b (two Peruvian rivers; 25 spp.); 3. Cairns and Yongue, 1966 (Douglas Lake region (USA); 31 spp.); 4. Ruthven, 1972 (South River, Virginia; 33 spp.); 5. Ilmavirta, 1988 (brown-water lakes, East Finland; 24 spp.); 6. Tong *et al.*, 1997 (three Antarctic lakes; 15 spp.); 7. Cairns, 1966a (Potomac River, Maryland; 15 spp.) (range 9–20 for benthic ‘Zoomastigina’). 8. Finlay *et al.* (1988) recorded at least 8 species on one occasion in Priest Pot (UK). These data provide a preliminary arithmetic mean value of 21 species. This may be an underestimate, as most of these authors did not use electron microscopy to discriminate species, especially of chrysomonads. Those who use EM usually record only chrysomonads, and if they also separately record heterotrophic species (e.g. Hällfors and Hällfors [1988], Kristiansen [1988], Jacobsen [1985], Kristiansen [1992], and Ikävalko *et al.* [1996]), they find that on average, heterotrophic species account for 21% of the total. Increasing our starting mean by this proportion brings us to 25 species. But few of the workers in our original list had investigated sediments, and few if any looked at the anaerobic or microaerobic layers – neither in the sediment nor in the water column. In a thorough study of an entire stratified water column with steep gradients of oxygen and reductants in a brackish water fjord, Fenchel *et al.* (1995) recorded 41 species, ten of which, from the microaerobic and anaerobic layers, had not previously been described. We conclude that a reasonable interim estimate range for local species richness of heterotrophic flagellates is 20–50. As a comparison, and according to Foissner (1991), local species richness of soil flagellates varies from “few to 47”.

^j Foissner (1992) produced a list of 282 species of heterotrophic flagellates used in the saprobic classification of fresh waters, compiled from various sources. This must be an underestimate of the global number of freshwater flagellates as it does not include those species that are excluded from saprobic classifications, although it exceeds the 208 species regarded by Foissner (1991) as being exclusively heterotrophic and living in soil. Patterson (pers. comm.) has recently reviewed 250 publications and found 750 nominal species of heterotrophic flagellates (excluding dinoflagellates). His ‘best estimate’ for the number within these 750 that are principally benthic marine heterotrophic species, is 250. See also Patterson *et al.*, 1989. Allowing for the existence of, (i) at least three other flagellate faunas: in soils, fresh waters, and the oceanic water column, as well as overlapping species complementing of all four faunas, (ii) the undoubted existence of a large number of synonyms, and (iii) the future discovery of new species; 350 species of heterotrophic flagellates in fresh waters is probably a realistic estimate.

are not simply components of the pond biota that act upon or respond to the way the ecosystem functions – rather they are continuously and intimately involved in feedback interactions – microbial activity and diversity are integral components of ecosystem function.

This study of a small pond illustrates some distinctive features of microbial (including protozoan) diversity that are not shared by the biodiversity of macroscopic animals and plants. These are:

- 1) Most species are ubiquitous on a global scale, and extinction of microbial species is unlikely.
- 2) Locally, many microbial species are rare or cryptic, and waiting for conditions to change in their favour. They may persist for long periods in this state of 'potential' rather than 'active' biodiversity.
- 3) Continuous reciprocal interactions between active microbial species and the physical-chemical environment establish microbial diversity as an integral part of ecosystem function. The 'seedbank' of microbial species ensures that micro-organisms always play their full part in ecosystem function (e.g. biogeochemical cycling). The concept of redundancy of microbial species has little meaning.

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