A critical review of the importance of rhizopods (naked and testate amoebae) and actinopods (heliozoa) in lake plankton

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Abstract

Planktonic sarcodines have mostly been overlooked or ignored in limnological studies mainly due to methodological and taxonomical problems. However, studies which have considered sarcodines indicate that amoebae and heliozoans could be important components of limnetic plankton communities, independent of trophic status and latitude of lakes investigated. Planktonic sarcodines are generally not as abundant as heterotrophic nanoflagellates, but, they may be as abundant or even more abundant than ciliates — the classical protozooplankton component of lakes. The contribution of sarcodines to annual mean protozooplankton biomass seems to be only a few per cent (1-15%). Sporadically however, sarcodines may be a very important constituent of plankton communities. Small forms (5 to 20 μm) seem to prevail among naked amoebae and heliozoans. In some lakes planktonic testaceans (*Difflugia*) may be abundant. Similar to marine and estuarine systems, naked amoebae seem to be often associated to particles and aggregates, and may be important functional components of lake snow. Rough estimations of the grazing impact of bacterivorous naked amoebae indicate their importance for the regulation of attached microbial communities on particles. In some cases amoeboid protists have been reported to be voracious consumers of algal blooms. Heliozoans consume autotrophic and heterotrophic nanoplankton, and omnivorous/carnivorous species have to be considered as potential grazers on other protozoans. It is suggested that planktonic sarcodines play an important role in the material flux of freshwater plankton communities as they do in marine plankton communities.

Key words: Zooplankton, Protozoa, Distribution, Biomass, Food web, Heliozoa, Amoebae, Testacea, Freshwater, Aggregates.

Résumé

**Revue critique sur l'importance des rhizopodes (amibes nues et amibes à thèque)
et des actinopodes (héliozoaires) dans le plancton des lacs**

Les sarcodinés planctoniques ont le plus souvent été oubliés ou ignorés dans les études limnologiques en raison surtout de problèmes méthodologiques et taxonomiques. Cependant, les études qui ont pris en compte

les sarcodinés indiquent que les amibes et les héliozoaires pourraient être des composants importants des communautés planctoniques lacustres, quels que soient l'état trophique et la latitude des lacs étudiés. Les sarcodinés planctoniques ne sont généralement pas aussi abondants que les nanoflagellés hétérotrophes, mais ils peuvent être aussi abondants, ou même plus, que les ciliés, le composant classique du protozooplancton des lacs. La contribution des sarcodinés à la biomasse protozooplanctonique moyenne annuelle semble ne représenter qu'un pourcentage faible (1-15%). Sporadiquement cependant les sarcodinés peuvent constituer une part très importante des communautés planctoniques. Les formes petites (5 à 20 µm) paraissent prévaloir parmi les amibes nues et les héliozoaires. Dans certains lacs les amibes à thèque (*Difflugia*) peuvent être abondantes. De même que dans les écosystèmes marins et estuariens les amibes nues semblent être souvent associées à des particules et des agrégats, et peuvent être des composants fonctionnels importants de la "neige" des lacs. Des estimations approximatives de l'impact de broutage des amibes nues bactérivores indiquent leur importance pour la régulation des communautés de microorganismes attachées aux particules. Dans certains cas, des protistes amiboïdes ont été signalés comme des consommateurs voraces des poussées algales. Les héliozoaires consomment du nanoplancton autotrophe et hétérotrophe, et les espèces omnivores/carnivores doivent être considérées comme des consommateurs potentiels des autres protozoaires. Il est suggéré que les sarcodinés planctoniques jouent un rôle important dans le flux de matière des communautés planctoniques d'eau douce comme ils le font dans les communautés planctoniques marines

Introduction

Recently, Caron and Swanberg (1990) gave an interesting review of the ecology of planktonic sarcodines. Their review dealt mainly with marine forms, since the classical planktonic sarcodines, radiolaria and some foraminifera, are marine protozoans. Skeleton bearing marine forms are often visible even in preserved net samples and have long been of taxonomic and recently also of ecological interest. In freshwater plankton naked forms — mainly very small in size — dominate, which have mostly been overlooked or ignored in quantitative plankton counts. Quantitative estimates regarding the importance of planktonic rhizopods and actinopods are therefore very rare in literature, and the idea of this paper is to point to the possibility that sarcodines may be important members of the plankton community in lakes, and that they should be considered for quantitative and functional estimates of the flux of organic matter within planktonic food webs. This short overview is intended to attract the attention of planktologists to this often ignored group of the zooplankton rather than to give a summary regarding the general importance of sarcodines in freshwater plankton.

Until the past decade protozooplankton was mainly a neglected component of limnetic zooplankton. The prevailing opinion was that "none of the other (protozoans excluding zooflagellates) groups has a significance that ordinarily may be accorded to the metazoan zooplankters" (Hutchinson, 1967, p. 491). This view has changed considerably since the pioneering work of Sorokin and Paveljeva (1972), who documented the great significance of planktonic protozoans in the material flux of a lake. Later on, major efforts were made in marine research (*cf.* Azam *et al.*, 1983; Fenchel, 1987; Laybourn-Parry, 1992). Today it is known that planktonic protozoans in lakes play a significant role in the regulation of bacterial density (*cf.* Güde, 1989), in nutrient recycling (*e.g.* Jürgens and Güde, 1990; Rothhaupt, 1992), and as a food source for metazoans (see reviews by Stoecker and Capuzzo, 1990; Arndt, 1993).

Among protozoans, the quantitative importance of ciliates (*e.g.* Nauwerck, 1963; Laybourn-Parry *et al.*, 1990; Müller *et al.*, 1991), heterotrophic nanoflagellates (*e.g.* Berninger *et al.*, 1991; Weisse, 1991) and heterotrophic microflagellates (*e.g.* Suttle *et al.*, 1986; Arndt and Mathes, 1991) have been considered. Recent reviews have been given by Laybourn-Parry (1992) and Riemann and Christoffersen (1993). Sarcodines have mostly been neglected in the recent investigations of the microbial food web in lake plankton.

However, the occurrence of sarcodines in the plankton of lakes has been known for one hundred years. Among sarcodines present in lake plankton mainly testate amoebae (*cf.* Grospietsch, 1972) and heliozoans (*cf.* Rainer, 1968; Page and Siemensma, 1991) have been given the most attention. For example the bentho-pelagic cycle of a species of *Difflugia* (Schönborn, 1962a) is often cited in textbooks. Naked amoebae were mainly thought to be unimportant (*cf.* Hutchinson, 1967), although Canter and Lund (1968) gave evidence for the importance of amoeboid protists as regulators of phytoplankton density in lakes. The reason for the neglect of sarcodines in protozooplankton counts during the last decade is mainly a methodological one. Dominant sarcodines in freshwater plankton are naked forms which are difficult to detect by means of the currently applied methods of fixation and counting (*cf.* Rogerson and Laybourn-Parry, 1992). An additional reason for their neglect was the assumption that most naked rhizopods need a substrate for feeding which was generally assumed to be not available in the plankton.

In this respect, the recent knowledge regarding the importance of macroaggregates in the sea ("marine snow") as major sites of microbial activity (*cf.* Sieburth *et al.*, 1976; Alldredge and Silver, 1988) brought new light into our knowledge regarding the functioning of the pelagic carbon and nutrient flux. These marine macroaggregates have been shown to be densely populated by naked rhizopods in the ocean (*cf.* Caron *et al.*, 1982; Caron *et al.*, 1986) and also in estuarine waters (Rogerson and Laybourn-Parry, 1992). Though the existence of detrital particles has also been shown for lakes, only the very recent results by Grossart and Simon (1993) have supplied evidence for the quantitative importance of macroscopic organic aggregates in lake plankton. This "lake snow" occurs in high concentrations and is densely inhabited by bacteria. Its function in the pelagic matter flux of lakes is most probably analogous to that of "marine snow". These macroaggregates in lake plankton are a potential habitat for naked rhizopods as it is known for the marine environment. Thus sarcodines will probably attract much more attention in future studies of the functioning of planktonic microbial food webs in lakes.

My interest regarding sarcodines in the plankton of lakes originated from my own studies by means of direct counts of protozoans in the highly eutrophic Lake Müggelsee, Berlin, where sarcodines had a very variable importance. Most of the results have been published elsewhere (Arndt and Mathes, 1991; Arndt and Nixdorf, 1991; Arndt *et al.*, 1993) including a description of methods used. Some of the data on sarcodines, which have not been considered in the earlier works explicitly, were extracted and are presented here among the data of other authors. When necessary methods used for sarcodine investigations are indicated in the text.

Methodological problems

As mentioned above, methodological problems seem to be one major reason for the neglect of planktonic sarcodines. Many naked amoebae need to be cultivated prior to species determination (*cf.* Page, 1976), because in most cases living organisms are required for the identification of naked amoebae and heliozoans. In some cases electronmicroscopical studies are necessary (*cf.* Page and Siemensma, 1991). Generally, the analysis of fixed samples will fail to give a reliable estimate of sarcodine abundance. It is generally recognized by microbial ecologists that the heterotrophic nanoplankton (HNAN) identified using epifluorescence microscopy (*e.g.* Caron, 1983) is composed of both flagellated and amoeboid protozoa.

A second problem associated with quantitative estimations of planktonic sarcodines is their abundance in the water column. Benthic sarcodines are known to occur in relatively high concentrations in freshwater (*e.g.* O'Dell, 1979), whereas only relatively low concentrations were expected from plankton samples (*e.g.* Kyle and Noblet, 1987). Therefore, up to now enrichment procedures mainly by means of cultivation and estimates of abundance using the "Most Probable Number" (MPN) technique were applied to estimate abundances of naked amoebae in field samples (*cf.* Davis *et al.*, 1978; Kyle and Noblet, 1986). The MPN-method relies on the growth of amoebae in a serially diluted water sample to estimate the original cell density. This method has mainly been applied for bacterivorous amoebae. When species can be recognized after fixation, enrichment can be obtained by means of sedimentation of samples, as it is done for phytoplankton. Heliozoa may sometimes be observed after fixation with Lugol solution, formaldehyde or glutaraldehyde (Page and Siemensma, 1991). Lewis (1985) published counts of planktonic amoeboid forms after Lugol fixation. However, counts of living organisms should be preferred, whenever it is possible. Otherwise many forms of the heterogenous groups of sarcodines will be overlooked. The only exception are testate amoebae which can be counted in fixed net or bottle samples (*e.g.* Pace, 1982; Meisterfeld, 1991), but even then live-observations significantly aided in the description of their functional importance (Meisterfeld, 1991). At high abundances of sarcodines, direct counts should be a suitable alternative or additional method. I had good experiences with live-counts made just after sampling using phase contrast microscopy and chambers on a temperature controlled microscopic table. The chambers were approximately 200 μm deep (obtained by coverslips which were adhered on a slide surrounding an opening where a droplet of known volume of lake water is placed and covered by a large cover slip).

Cultivation methods and direct counts have both advantages and disadvantages. Direct counting is very time consuming when abundances are low; it needs a lot of time directly after sampling; only a limited number of samples can be handled at the same time; often only rough taxonomical differentiations can be made. However, organisms can be observed in their approximate natural habitat; feeding modes and food vacuoles can be observed; resting stages are not counted. The disadvantage of cultivation techniques is that culture conditions may be selective and excysted organisms may be counted. Therefore, both of the methods seem to reveal minimal estimates. Baldock (1986) compared these methods with counts of fixed samples of fine sediments and found a variable success of each method for the different protozoan groups. In her estimates of small naked amoebae, direct live-counts gave better results than the other two methods. A recommendable alternative seems to be the procedure recently applied by Rogerson and Laybourn-Parry (1992), who used an enrichment by gentle centrifugation followed by a cultivation of fifty subsamples of known volume (5 µl). Subcultures were not necessary.

A third problem is the small size of the dominant sarcodines in plankton samples which makes their detection difficult. Small sized sarcodines were mainly overlooked in quantitative studies until the work of Rogerson and Laybourn-Parry (1992). Their observations in a Scottish estuary showed that on annual average, about one half of all naked amoebae have locomotive forms smaller than 10 µm. For lake plankton such observations are missing. My own observations regarding the annual mean size-distribution of naked amoebae and heliozoans in the shallow highly eutrophic Lake Müggelsee (Berlin) are shown in Figure 1. It is evident that in lake plankton, too, small forms may dominate. As a mean, about 50 percent of naked amoebae had an equivalent spherical diameter (body dimensions were determined by means of an ocular micrometer and a calibrated focus, respectively) smaller or equal to 10 µm. Among planktonic heliozoans, which were not yet investigated in this respect, small forms also dominated. The bimodal distribution was due to *Actinophrys sol* and other species which dominated in large size classes (Fig 1). Both of the sarcodine groups had significantly different mean annual size distributions in the three successive years (Fig. 1). This may indicate a different species composition and also indicates that size distributions must be determined for calculations of sarcodine biomass. Biomass of heliozoans and naked amoebae was dominated by the 15 to 20 µm size group. These results on the sarcodine size distribution are confirmed by recent studies of protozooplankton in many different north German lakes by Mathes (pers. comm.). Though, further studies are necessary, the prevalence of very small forms among sarcodines seems to be characteristic for lake plankton.

It is widely accepted that routine sampling of protozooplankton requires short-term (few days) intervals of sampling in order to estimate seasonal or annual fluctuations. In this respect, the registration of planktonic occurrence of naked sarcodines (naked amoebae and heliozoans) seems to be especially sensitive. There are reports in literature describing the appearance and disappearance (encystment) of a voracious algivorous amoebae within some days (Cook *et al.*, 1974). It seems that some naked amoebae are specialized feeders (for review see Sandon, 1932) which are obviously
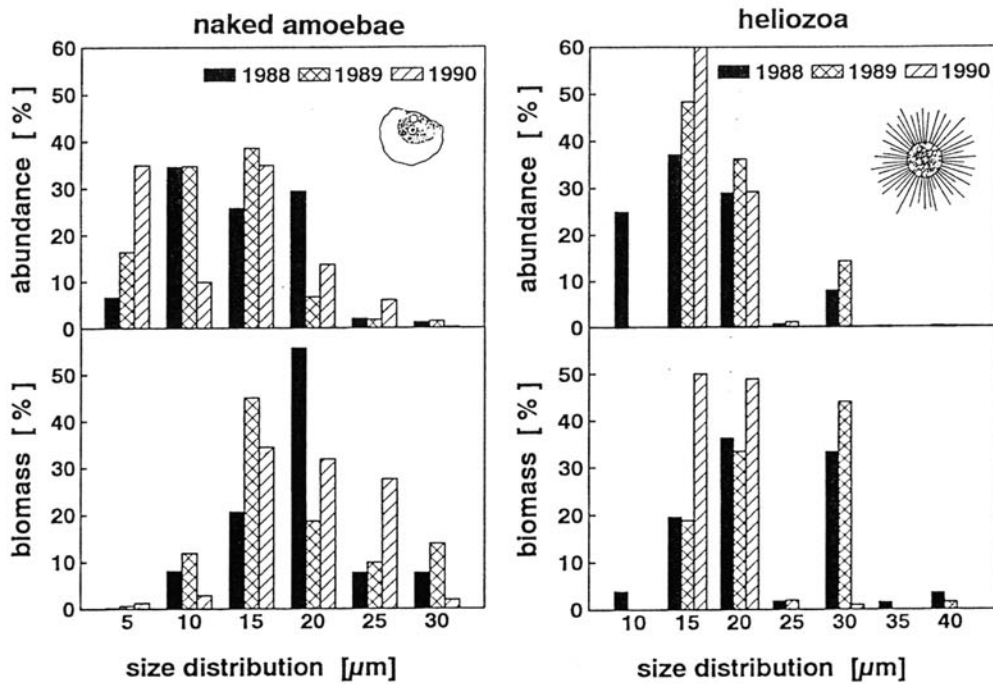
Fig. 1. Size distribution of naked amoebae and heliozoans in plankton samples of Lake Müggelsee, Berlin. Annual means (sampling interval generally 1-2 weeks) are shown for the years 1988 (n = 43 samplings per year), 1989 (n = 32), and 1990 (n = 29), resp. The upper panels show size distributions regarding the abundance, the lower panels those regarding the biomass. The percentages of abundance and biomass were calculated per size group per year for a total amount in the respective year. Equivalent spherical diameters were calculated from body dimensions.

able to respond to changing conditions within very short periods of time. Amoebae concentrations in integrated plankton samples from Lake Müggelsee changed by up to two orders of magnitude within one week (*cf.* Fig. 2). Rainer (1968) reported a very patchy distribution of heliozoans. It means that care has to be taken when planning sampling programs for planktonic sarcodines.

A wider application of molecular methods may help to solve the above mentioned problems in the future. One tool for detection of viable sarcodines will be monoclonal antibodies. Another recent technology which may be applied to detect and count sarcodines in field samples may be the use of gene probes. Both of these methods will be applied for pathogenic amoebae (*cf.* Tyndall and Ironside, 1990), but may be used for other free-living sarcodines in near future (Brown, pers. comm.).

Taxonomic composition of sarcodines in lake plankton

Research on planktonic sarcodines is currently the domain of specialists. These amoeboid protists are generally not included in routine plankton records. The

exception are testate amoebae which are, due to preservation of their taxonomic
relevant tests with standard fixatives, often reported in quantitative records from river
plankton (*e.g.* Bereczky, 1978/79, 1991) as well as from the plankton of very different
lakes and estuaries (*e.g.* Eng, 1970; Pace, 1982; Hunt and Chein, 1983; Barbieri and
Godinho Orlandi, 1989).

In addition to the methodological problems mentioned above, the sarcodines offer
considerable taxonomical difficulties, which may deter planktologists from considering
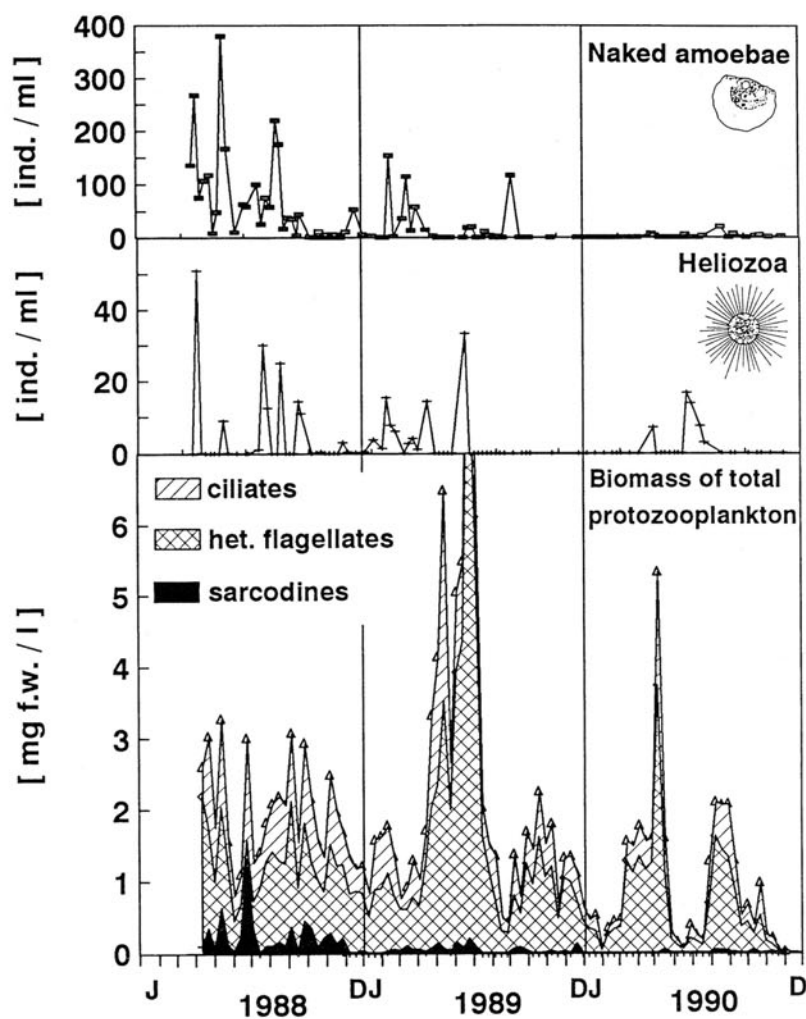
Fig. 2. Seasonal dynamics of sarcodines in the plankton (integrated samples of the mixed surface water)
of Lake Müggelsee, Berlin. Upper panels: Seasonal changes in the abundance of naked amoebae and
heliozoans. Lower panel: Seasonal changes in the biomass of the different groups of
protozooplankton.

sarcodines quantitatively. Sarcodines are a polyphyletic group and in many respects opinions regarding their systematics have not yet been settled. This is illustrated by a comparison of the systematics in Lee *et al.* (1985) and Margulis *et al.* (1990). In addition, many floating and limax forms of naked amoebae have originally been described as different species (*cf.* Bovee and Sawyer, 1979; Page and Siemensma, 1991); and even some stages in the life-history of dinophyceans were described as separate species of naked amoebae or heliozoa (*cf.* Popovsky and Pfiester, 1982). Some naked amoebae are flagellated or have flagellated stages. The potential of many forms to change their morphology is an additional problem for an ecologist dealing with these beautiful planktonic organisms. At present, however, even rough quantitative estimates of sarcodine occurrence would greatly aid in our understanding of their ecological importance. With some experience amoeboid forms occurring in plankton samples can be sorted for rough taxonomic groups, sometimes to a certain genus or species. Those forms, which cannot be assigned, can be sorted to unidentified groups divided, if possible, into functional groups (*e.g.* predominantly bacterivores, predominantly algivores, etc.). But, whenever possible, ecological studies should include the knowledge of species. Unfortunately, there is a tendency to use only electron microscopical studies to separate species (*cf.* Page and Siemensma, 1991), which is difficult to apply for ecological studies. Molecular methods will help in the near future.

Table I may serve as a preliminary orientation regarding the systematic position of taxa of amoeboid protists, with special attention to those taxa which have been more or less commonly reported from limnetic plankton samples. The systematics of Page and Siemensma (1991) and Sleigh (1991) were mainly followed. Results of molecular biological investigations will certainly change the systematics of sarcodines in the near future. In many cases the systematic position is uncertain. For instance, ciliophryids, which can be abundant in brackish waters (Andersen and Sorensen, 1986), are either grouped to heliozoans (*cf.* Febvre-Chevalier in Margulis *et al.*, 1990; Page and Siemensma, 1991) or — as pedinellids or helioflagellates — to heterotrophic flagellates (*e.g.* Preisig *et al.*, 1991; Sleigh, 1991). A comprehensive overview on amoebae-like and heliozoan-like flagellates was recently given by Patterson and Larsen (1991).

Amoebae and heliozoans are the limnetic representatives of amoeboid protists. Amoebae consist of forms possessing no test (naked amoebae) or a simple mucoproteinaceous or proteinaceous test (testate amoebae) with more or less simple pseudopods (in some publications the term amoebae refer only to naked amoebae). The structure and shape of the tests is mostly species-specific. Naked forms are distinguishable only when alive by the cell size and shape, and the morphology of the pseudopods of the locomotive and floating forms. Often additional characters are necessary for the differentiation of species or genera such as the occurrence of flagellated forms, the presence and morphology of cysts, the appearance of the nuclear apparatus or other parts of the ultrastructure. Actinopods are separated from rhizopods by the presence of axopods which are thin pseudopodia possessing microtubules which give the axopods their rigid character. Heliozoans among actinopods are characterized by the typical ultrastructure of their axopods. Temporarily, they may have pseudopodia or the very thin filopodia. Some heliozoans may have siliceous or organic

TABLE I. – Taxonomic orientation regarding the groups of rhizopods and actinopods in lake plankton (some representative genera are named, those which are often reported from plankton are underlined)

RHIZOPODA
    Heterolobosea
        e.g. Vahlkampfiidae (*e.g.* <u>*Vahlkampfia, Naegleria*</u>)
    Lobosea
      Gymnamoebia
          e.g. Amoebidae (*Chaos,* <u>*Amoeba*</u>), Hartmanellidae (<u>*Hartmannella, Saccamoeba*</u>),
          Thecamoebidae (*Thecamoeba*), Vanellidae (<u>*Vanella, Platyamoeba*</u>), Paramoebidae
          (<u>*Mayorella, Paramoeba*</u>), Vexilliferidae (<u>*Vexillifera*</u>), Acanthamoebidae (<u>*Acanthamoeba*</u>)
      Testacealobosia
          e.g. Arcellidae (<u>*Arcella*</u>), Centropyxidae (<u>*Centropyxis,* Cyclopyxis</u>), Difflugiidae (<u>*Difflugia,*</u>
          Cucurbitella), Nebelidae (*Nebela*)
    Caryoblastea
          e.g. Pelomyxidae (*Pelomyxa*)
    Eumycetozoea (cellular and syncytial slime moulds)
    Plasmodiophorea (intracellular parasites in plants)
    Filosea
          e.g. Nucleariidae (*Nuclearia*), Vampyrellidae (<u>*Vampyrella*</u>), Euglyphidae (<u>*Euglypha,*</u>
          <u>*Trinema*</u>), Cyphoderiidae (<u>*Cyphoderia*</u>), Paulinellidae (<u>*Paulinella*</u>)
    Granuloreticulosea
          e.g. Athalamida (*Biomyxa*), Monothalamida (*Gromia*), Foraminiferida
    Xenophyophorea (amoeboid forms with branched organic tests from deep-sea sediments)

ACTINOPODA
    Heliozoea
          Actinophryida (<u>*Actinophrys, Actinosphaerium*</u>), Ciliophryida (<u>*Ciliophrys, Actinomonas*</u>),
          Desmothoracida (*Clathrulina*), Centrohelida (<u>*Acanthocystis, Raphidiophrys, Raphidocystis*</u>),
          Dimorphida (*Dimorpha*)
    Polycystinea
    Phaeodarea
    Acantharea

spicules. In some species, unfortunately, only the morphology of these spicules is known (*e.g.* Dürrschmidt, 1987). Generally, live specimens are needed for species determinations. The most recent key for the determination of limnetic sarcodines was given by Page and Siemensma (1991).

Many typical marine forms such as foraminifera and radiolaria generally do not occur in freshwater. Naked amoebae can be abundant in the plankton of the open ocean (*cf.* Caron and Swanberg, 1990), in estuarine waters (*cf.* Rogerson and Laybourn-Parry, 1992) and also in limnetic waters (*cf.* Kyle and Noblet, 1987). Testate amoebae are typical for limnetic waters (*cf.* Grospietsch, 1972), but may also occur in significant numbers in estuarine waters (*e.g.* Eng, 1970). Heliozoans are common components of fresh waters. They occur in lakes (*cf.* Rainer, 1968), and small brooks and rivers (*e.g.* Rainer, 1968; Arndt, 1991b), but may be also abundant in estuarine (*e.g.* Tobiesen, 1991; Arndt, 1991a) and marine waters (*cf.* Caron and Swanberg, 1990).

There is only meagre information available regarding species composition (even lists of species or dominant genera occurring in special habitats are very sparse). Some comments on taxonomic composition of the three sarcodine groups are given below.

Naked amoebae: By means of the MPN-technique Kyle and Noblet (1986,1987) found vahlkampfiid, hartmannellid, and acanthamoebid amoebae dominant among thermotolerant (cultured at 37°C) species of eutrophic waters in the USA. In direct counts of river plankton (Danube), amoebid, vahlkampfiid, and paramoebid genera were recorded (Bereczky, 1978/79). Investigations on estuarine planktonic amoebae showed a dominance of vanellid (*Platyamoeba*, *Vanella*), paramoebid (*Neoparamoeba*, *Mayorella*), and acanthamoebid (*Acanthamoeba*) amoebae (Rogerson and Laybourn-Parry, 1992). Laybourn-Parry *et al.* (1990) found members of the genera *Vanella*, *Rhogostoma* and *Vexillifera* by means of the MPN-technique in the plankton of the eutrophic Esthwaite Water, English Lake District. My own observations by means of live-counts in plankton samples of Lake Müggelsee indicated the occurrence of vahlkampfiid, vanellid, hartmannellid, and paramoebid amoebae among other unassigned forms. Most of these amoebae were very small (*cf.* Fig. 1).

Testate amoebae: In contrast to our limited knowledge concerning the species distribution of naked amoebae, notes on the occurrence of testacean species are to be found in various zooplankton records from lakes and ponds (*cf.* Grospietsch, 1972) as well as in running waters (*e.g.* Bereczky, 1978/79). Maes (1989) found 14 testacean species in a polluted brook-pond system. In the well-studied Lake Stechlin, Germany, about half of the recorded testacean taxa of that lake may occur in plankton samples. However, only some *Difflugia* species and *Arcella vulgaris* occurred as active planktonic forms, passive transport by water currents was the reason for the planktonic occurrence of the other species (*cf.* Schönborn, 1962b). The most common genus reported from plankton samples is *Difflugia*. Records of the often mentioned *D. limnetica* (may be either a synonym of *D. hydrostatica* or *D. pseudolimnetica*) have to be reanalysed taking into account the recent taxonomical review by Ogden and Meisterfeld (1989). The second most common genus is *Arcella*. Several other typical benthic forms were found occasionally in plankton samples (*cf.* Grospietsch, 1972). Many small (< 30 μm) testate, mainly filose amoebae may have been underestimated in plankton records, since they may pass commonly used plankton nets (50 μm mesh size) and are difficult to determine.

Heliozoa: Most studies on planktonic heliozoans have dealt mainly with taxonomic problems rather than the relative contribution of each taxa (*e.g.* Dürrschmidt, 1987; Siemensma and Roijackers, 1988). Rainer (1968) gave an interesting overview regarding his ecological investigations. In his semiquantitative records from a dystrophic water he found most frequently *Actinosphaerium eichhorni*, *Acanthocystis penardi*, *Pompholyxophrys punicea*, and *Raphidiophrys intermedia*. These are followed in order of relative abundance by *Actinophrys sol* and *Acanthocystis turfacea*. Generally, *Actinosphaerium eichhorni* and *Actinophrys sol* are mentioned in plankton records. Though these species are common, these records may be biased due the relatively easy determination of these species compared to other heliozoan species.
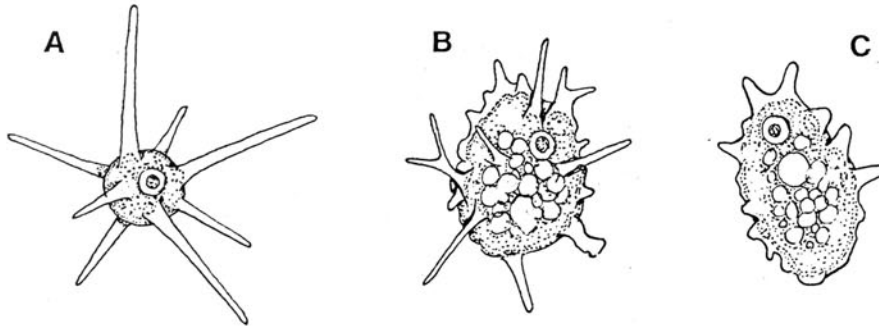
Fig. 3. Morphological changes of *Mayorella corlissi*. A: floating form; B: form at beginning locomotion after floating; C: locomotive form (after Sawyer, 1975). These morphological changes are typical for many genera of naked amoebae occurring in freshwater plankton.

In Lake Müggelsee, for instance, centrohelid heliozoans were sometimes more common than actinophryid heliozoans.

The benthic and pelagic life of many sarcodines may be closely connected. Many amoebae can change their form from a locomotive to a floating form and vice versa. These changes can occur within a few minutes. The formation of floating forms can be connected with the formation of gas vacuoles (*e.g.* Bovee, 1961). Figure 3 illustrates the different morphology of the locomotive and floating form of a *Mayorella* species (after Sawyer, 1975). Floating forms are generally characterized by the presence of relatively thin pseudopods which are spread in a three-dimensional way around the center of the protoplasm. Some testate amoebae can change between a benthic and pelagic life in the course of a year (see below). Many heliozoans species may occur in the plankton or associated with macrophytes (Rainer, 1968). Thus, species lists of benthic and planktonic samples may not deviate significantly. Kyle and Noblet (1986, 1987) found clear similarities between the thermotolerant naked amoebae fauna in benthic and planktonic samples.

Distribution and abundance of sarcodines in lake plankton

Mechanisms for planktonic life

Heliozoans have the appearance of planktonic organisms (though the majority should be benthic or epibenthic according to Rainer, 1968), but lobose amoebae look mostly like typical benthic organisms. However in all groups of sarcodines mechanisms have been evolved to populate the planktonic habitat. First, there are morphological features: long axopods of heliozoans may aid in planktonic dispersion; many amoebae have the ability to form floating (see Fig. 3) or flagellated stages (*e.g.* some vahlkampfiid amoebae). Second, special physiological mechanisms such as

the formation of gas vacuoles/bubbles and the production of fat droplets are known from all limnetic groups of sarcodines to support planktonic life (*e.g.* Bovee, 1961; Schönborn, 1962a; Meisterfeld, 1991). Third, behavioural mechanisms are known such as attachment to particles with low sinking speeds, attachment to particles with gas vacuoles (blue-greens), attachment to the surface microlayer, migration (*e.g.* flagellated amoebae). The ability of sarcodines to make short-term changes of habitat between benthic or epibenthic life and planktonic life has to be considered when analysing the distribution of planktonic sarcodines.

Abundances of planktonic sarcodines

In Table II some data on abundances reported from studies in very diverse habitats have been listed to give an impression what abundance may occur in the plankton community. It is evident that naked amoebae can be by far the most abundant sarcodines in plankton. In limnetic waters, heliozoans can occasionally reach the same or even higher abundance. The listing in Table II may be biased in several respects. First, sarcodines may have been only reported in literature when they were abundant. Second, most results regarding naked amoebae were from cultivation methods, which certainly underestimated the real abundance. Third, only a very few habitats have been sampled and analysed in detail, thus no overall generalization can be made. Regarding freshwater testaceans, only a few examples were selected.

In all studies, where planktonic sarcodines were given special attention, they were found to be abundant, at least sporadically. This is true for all the diverse habitats studied, from the open ocean to Antarctic freshwater lakes. The great variation of reported abundances may reflect methodology as well as true variations in abundance. However, there seems to be a gradient from a low mean abundance (up to 150 ind.l^{-1}) in oligotrophic marine and freshwaters to a high abundance (sometimes more than 5,000 ind.l^{-1} as an annual mean abundance) in highly eutrophic estuarine or freshwater habitats. Laybourn-Parry *et al.* (1991) found amoebae concentrations in an Antarctic lake that were in the same range as in a eutrophic temperate lake. They explained this unexpected result by the special significance of floccules in the Antarctic lake that originated from benthic mats. In the following special consideration will be given to aggregates.

Lake snow and the surface microlayer as important habitats

It is evident from Table II that high concentrations of sarcodines, mainly naked amoebae, can occur on aggregates. Both large dead organic particles and the surface microlayer, are known to support significantly higher numbers of microorganisms than the surrounding water. However, our knowledge regarding the quantitative importance of these habitats has increased dramatically in the last 15 years. Most studies have been carried out in the ocean (for reviews see Alldredge and Silver, 1988, and Caron,

1991). Concentrations of picoplankton on aggregates can be two and more orders of magnitude higher than in the surrounding water, thus providing concentrated food patches for bacterivorous protozoans, including sarcodines (*e.g.* Caron *et al.*, 1982). This seems to be true also for the marine surface microlayer (*cf.* Sieburth *et al.*, 1976). In freshwaters, neither of these habitats have been well-studied quantitatively, although the general importance of the surface microlayer is well-known (for review see Guthrie, 1988). Naked amoebae and testaceans (*Arcella*) are known to be frequent inhabitants of the hyponeuston under calm weather conditions. Kyle and Noblet (1986) reported a significant increase of abundance (up to four times) of thermotolerant naked amoebae in the surface microlayer of a pond. Amoebae could be accumulated due to the abundance of nutrients which may support high rates of reproduction and excystment of air-borne cysts.

The importance of macroscopic organic aggregates in lakes have long been overlooked. However, the very recent results by Grossart and Simon (1993) gave evidence for the quantitative importance of macroaggregates in lake plankton, too. This "lake snow" occurs in relatively high concentrations (*e.g.* up to 50 particles larger than 3 mm per liter) in the mesotrophic large Lake Constance. These aggregates were densely inhabited by bacteria (about 100 times higher concentration than in the bulk water). On the basis of abundance and dry weight lake snow aggregates comprised 20-40% of the detrital particulate organic carbon and were important sites of carbon and nutrient cycling (Grossart and Simon, 1993). These particles should be ideal sites especially for naked amoebae as known from marine habitats. Laybourn-Parry *et al.* (1991) pointed to the importance of detrital flocs in an ultraoligotrophic Antarctic lake; amoebae may be concentrated in flocs and heliozoans may move between them. A quantitative study was done by Rogerson and Laybourn-Parry (1992) regarding the particle association of planktonic amoebae in the Clyde estuary. They found that the majority of amoebae was retained on a sieve with a mesh size of 15 µm (scanning their Fig. 5: 53 ± 32%, n = 6, were retained at stations in the Clyde; 72 ± 37%, n = 6, were retained at Striven). I performed similar experiments in Lake Müggelsee. A sieve of 28 µm mesh size was used. Naked amoebae were registered by direct counts of plankton samples before and after passing the sieve. Up to 76% (mean 39% ± 33%, n = 8, samplings from April through August, 1988) of the amoebae were retained in the size fraction larger than 28 µm, although very small forms prevailed. Since this is a minimum estimate due to the possibility that amoebae lose attachment during filtration, this indicates that in limnetic waters, too, large particles seem to be an important site of sarcodine activity. This view is supported by the results of Kyle and Noblet (1986, 1987), who found higher numbers of thermotolerant amoebae in vertical strata with a higher light attenuation.

In Table III enrichment factors of different protozoan groups on aggregates are shown. The data by Caron *et al.* (1986) are compared with my own observations from the highly eutrophic Lake Müggelsee (Berlin) and the mesotrophic alpine Lake Mondsee (Austria). Data for these lakes were obtained by the sampling of macroaggregates (mixed samples from various sites of the lake) by means of a sterilized beaker from aggregations in the surface water due to wind induced

TABLE II. – Abundance of naked and testate amoebae and heliozoans observed in different pelagic marine and freshwater habitats (MPN: Most Probable Number technique, DC: direct counts)

Habitat description, comments	Taxonomic group	abundance ind.l⁻¹

Marine water

North Atlantic, Caribbean Sea, Narragansett Bay (Davis *et al.*, 1978)

subsurface plankton, MPN	naked amoebae	1-10
surface microlayer, MPN	naked amoebae	10-100
mean in upper 5 µm, MPN	naked amoebae	1,413

North Atlantic, surface samples (Caron *et al.*, 1986), mean values for different regions recalculated from their tables 3 and 4)

subsurface plankton, MPN	naked amoebae	3.6-37
abundance within macroaggregates	naked amoebae	1,900-53,200

Pacific, subantarctic stations, different depth (Kopylov and Sashin, 1988)

plankton, different stations, DC	naked amoebae	0-30,000
max. at one station at 160 m	naked amoebae	68,000

East China Sea, seasonal study (Tan *et al.*, 1978, cited in Caron and Swanberg, 1990)

Sticholonche zanclea, DC	heliozoa	0.001-100

Brackish water

Clyde estuary, Scotland, seasonal study at different stations (Rogerson and Laybourn-Parry, 1992)

plankton, range (annual mean)	naked amoebae	0-43,000
cultivation of 50 subsamples		(8,300)

Ponggol estuary, Singapore, seasonal study (Eng, 1970)

Difflugia sp., DC	testate amoebae	0-657

Limfjorden, Denmark, maximum abundances recorded in seasonal studies in plankton samples (Andersen and Sorensen, 1986)

Actinomonas mirabilis, DC	helioflagellate	400,000
Ciliophrys marina, DC	helioflagellate	200,000

Freshwater

River Frome, chalk stream in Dorset, England, seasonal study, mean value (Baldock *et al.*, 1983)

plankton, MPN	naked amoebae	2,000

River Danube, at Göd near Budapest, Hungary, mean value of 7 samplings in autumn (recalculated from Table 1 and 2, Bereczky, 1991)

Amoeba spp., DC	naked amoebae	4.4
Arcella, *Difflugia*, DC	testate amoebae	10.9

Willard's Pond, warm monomictic lake in South Carolina, seasonal study of thermotolerant amoebae (cultured at 37°C, Kyle and Noblet, 1986)

plankton samples, MPN	naked amoebae	40-1,800

Lake Issaqueena, other comments as above (Kyle and Noblet, 1987)

plankton samples, MPN	naked amoebae	80-2,240

Antarctic lakes, 12 freshwater and slightly saline lakes (Laybourn-Parry and Marchant, in press)

plankton samples, DC	naked amoebae	0-150

Lake Oglethorpe, a small monomictic eutrophic lake in Georgia (Pace, 1982)

Difflugia , DC	testate amoebae	0-329

Rio Grande Reservoir, a eutrophic subtropical reservoir in Brazil, seasonal plankton study (Barbieri and Orlandi, 1989)

Difflugia, DC	testate amoebae	0-240

Old sand pit in the lower Rhine area, Germany (Meisterfeld, 1991)

Difflugia hydrostatica, max., DC	testate amoebae	2,200

Crooked Lake, Antarctica, ultraoligotrophic, seasonal study, mean abundance in the water column (Laybourn-Parry *et al.*, in press)

plankton, DC	naked amoebae	100-150
	heliozoa	10-160

Esthwaite, eutrophic lake in the English Lake District, seasonal study (Laybourn-Parry *et al.*, 1990)

plankton, MPN	naked amoebae	10-50
plankton, DC	heliozoa	0-1,200

Neumühler See, mesotrophic lake in Mecklenburg, Germany, seasonal study (25 plankton samplings/year, Mathes, 1992 and unpublished)

DC, range and (annual mean)	naked amoebae	0-5,560 (222)
	testate amoebae	0-43.3 (3.6)
	heliozoans	0-77,520 (5,183)

Müggelsee, highly eutrophic shallow lake in Berlin, Germany, seasonal study of integrated plankton samples (43, 32, 29 samplings/year, resp., Arndt, this study)

DC, range and (annual mean)	1988	naked amoebae	0-380,000 (62,700)
	1989		0-153,700 (19,540)
	1990		0-20,000 (1,970)
	1988	testate amoebae	0
	1989		0-50 (1.6)
	1990		0-5.8 (0.2)
	1988	heliozoa	0-50,900 (4,670)
	1989		0-33,300 (2,820)
	1990		0-16,700 (1,660)
max. in an *Aphanizomenon* patch		naked amoebae	12,000,000

turbulences. Protozoans were counted by live-counts. The volume of macroaggregates was estimated after sedimentation in a calibrated glass cylinder. Though these studies have to be verified by future experiments, the comparison in Table III indicates that enrichment factors of marine and freshwater habitats may be in the same order of magnitude. Highest enrichment in the lakes was found for naked amoebae. Caron (1991) compared the enrichment of HNAN (heterotrophic nanoplankton which includes mainly flagellates and also naked sarcodines) on macroscopic detrital aggregates in lakes of different trophy. He and his co-workers reported a decreasing enrichment factor of HNAN with increasing trophy. My studies regarding the

TABLE III. – Enrichment of protozoans in macroaggregates from marine and limnetic surface waters. Comparison of Most Probable Number estimates from the North Atlantic (data from Caron *et al.*, 1986) and direct count estimates from the highly eutrophic Lake Müggelsee (Berlin) and the mesotrophic Lake Mondsee (Austria, Arndt, unpubl.). The enrichment factor is the ratio of the average density of a population in the macroaggregates to its density in the surrounding water.

| *Sampling site* | Enrichment factor | | |
	amoebae	het. flagellates	ciliates
North Atlantic			
Continental Shelf	413	476	-
Slope	586	508	-
Gulf Stream	2280	7640	9080
Sargasso Sea	6190	18400	77400
Freshwater			
Lake Müggelsee (May)	742	35	120
Lake Mondsee (October)	596	545	327

enrichment of flagellates and ciliates (see Table III) indicate the same tendency. However, the actual quality of aggregates during sampling may play a very significant role. General conclusions regarding the influence of the trophy on the enrichment of protozoans on aggregates in lake plankton require a much larger set of data than we have today. It seems that floating particles are a major site for naked amoebae rather than other sarcodines, though, Laybourn-Parry *et al.* (1991) also observed heliozoans moving between floccules.

Aggregates in lake plankton, although different in origin and composition from marine aggregates, seem to be similar in their character and function to marine aggregates (*cf.* Grossart and Simon, 1993), and that they form suitable substrates and places of enrichment for sarcodines comparable to marine waters. Originally, increased biological activity on aggregates was considered as a special adaptation to the nutritionally diluted marine environment (*cf.* Goldman, 1984). However, present knowledge indicates that high biological activity on aggregates seems to be typical for plankton communities whether in the Sargasso Sea, in an Antarctic lake, in a large mesotrophic lake or in a shallow highly eutrophic temperate lake.
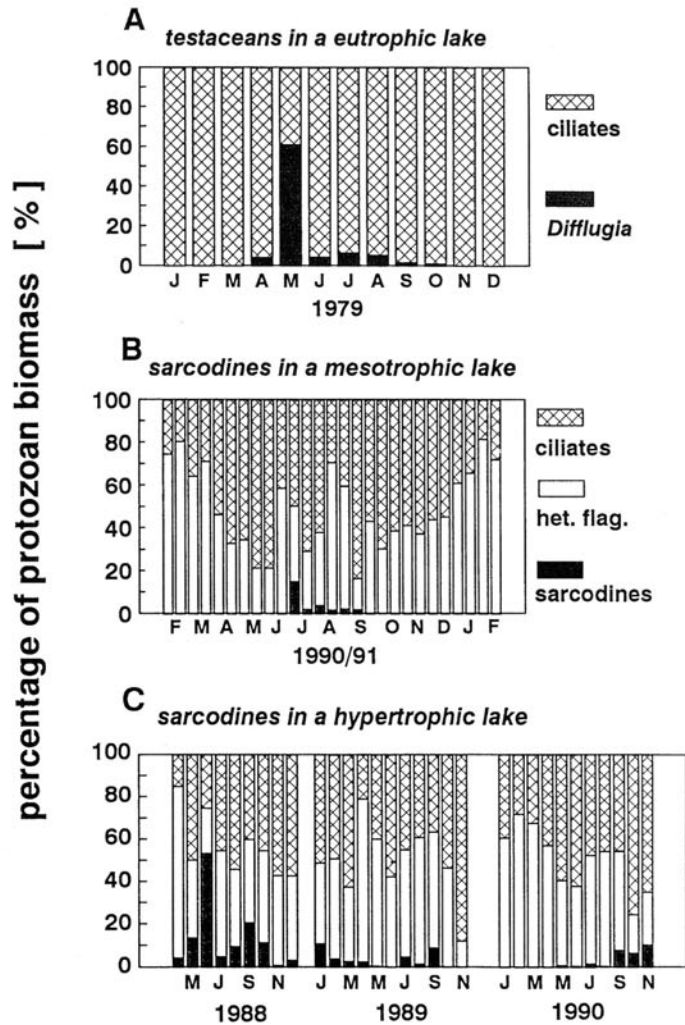
Seasonal distribution

Figures 4 and 5 summarize results of different authors regarding the seasonal cycle of planktonic sarcodines. In the water bodies of the temperate zone, the maximum abundance generally occurs in the summer months. The shallow Lake Müggelsee is probably an exception, since wind induced resuspensions may have disturbed this pattern (Fig. 2). The bentho-pelagic cycle of *Difflugia* in north German lakes described by Schönborn (1962a, *cf.* Fig. 4A) may be the best studied seasonal cycle of a limnetic planktonic sarcodine. Excystment and multiplication occur in early spring in the
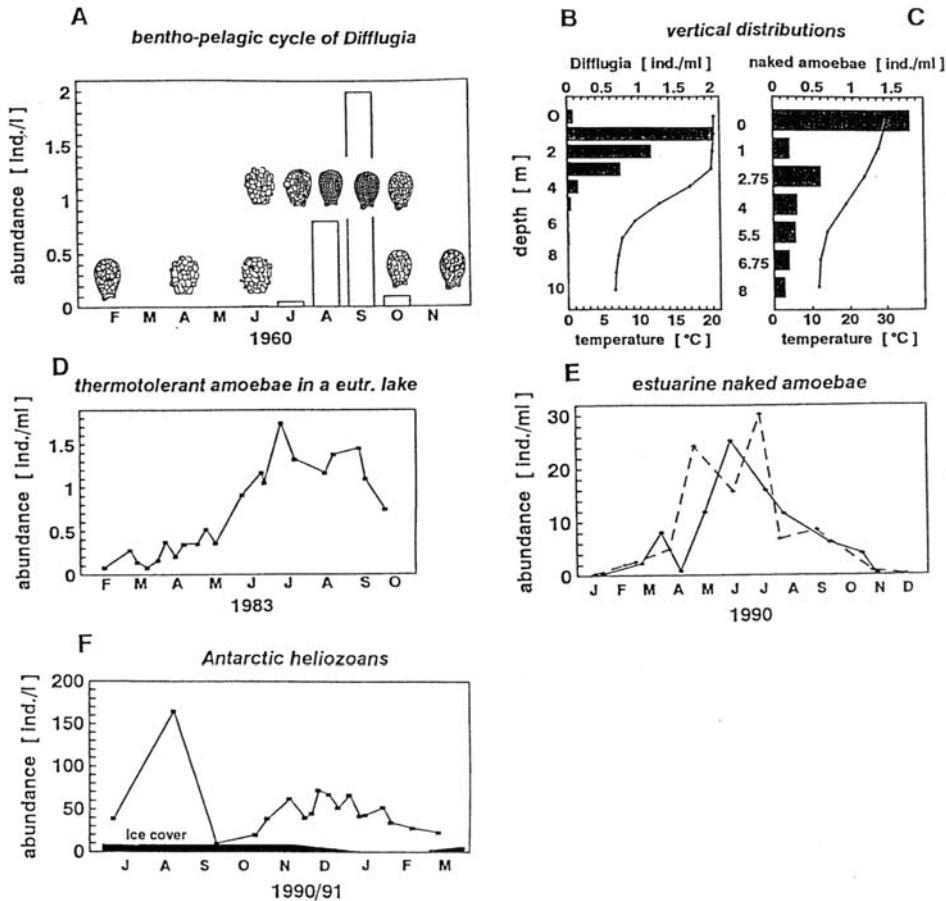
Fig. 4. Seasonal and vertical distribution of planktonic sarcodines observed by various authors. A: Bentho-pelagic cycle of *Difflugia* in Lake Stechlin, Germany. Bars indicate the abundance, figures indicate changes in the morphology of tests (modified after Schönborn, 1962a). B: Vertical distribution of *Difflugia hydrostatica* in a sand pit near River Rhine, Germany. Abundance is indicated by black bars (modified after Meisterfeld, 1991). C: Vertical distribution of thermotolerant naked amoebae in Lake Issaqueena, USA, in July (modified after Kyle and Noblet, 1987). D: Seasonal changes in the abundance of thermotolerant amoebae (MPN-technique at 37°C) from the surface water (deep water station) in Lake Issaqueena (modified after Kyle and Noblet, 1987). E: Seasonal changes in the abundance of naked amoebae at two combined stations (broken and continuous line) in the Clyde estuary, Scotland (modified after Rogerson and Laybourn-Parry, 1992). F: Seasonal changes in the abundance of heliozoans in the ultraoligotrophic Crooked Lake, Antarctica (modified after Laybourn-Parry *et al.*, in press).

Fig. 5. Seasonal changes in the composition of protozooplankton biomass observed by various authors. A: Seasonal changes in the contribution of *Difflugia* to the biomass of ciliates and testaceans in the eutrophic Lake Oglethorpe, USA (data from Pace, 1982). B: Seasonal changes in the contribution of sarcodines to total protozooplankton biomass in the mesotrophic Lake Neumühler See, Germany (modified after Mathes, 1992). C: Seasonal changes in the contribution of sarcodines to total protozooplankton biomass in the hypertrophic Lake Müggelsee, Berlin (modified after Arndt *et al.*, 1993).

benthos. In June, benthic specimens become planktonic via the formation of fat droplets and gas bubbles. *Difflugia* abundance increases through the summer and peaks in September. The subsequent decline in abundance is due to sinking, partly as a result of an increase in density as fat droplets are metabolized. The majority of sinking

specimens die, but some form a cyst in their tests and others remain active in the benthos throughout the winter. The morphology of the tests changes in the course of the bentho-pelagic cycle according to the building material available (*e.g.* Casper and Schönborn, 1985). Drastic seasonal changes of *Difflugia* species have been observed in very different lakes ranging from subtropical (*e.g.* Barbieri and Godinho Orlando, 1989) to temperate waters (*e.g.* Pace, 1982). Naked amoebae also appear to be more abundant during summer months (Kyle and Noblet, 1986, 1987, *cf.* Fig. 4D). Even under a thick icecover, Laybourn-Parry *et al.* (in press) reported a significant number of amoebae and heliozoans among the plankton. Much more data, especially regarding species specific annual cycles, are necessary for a better understanding of the ecology of planktonic sarcodines.

Vertical distribution

The vertical distribution of planktonic sarcodines is poorly known (two examples are shown in Fig. 4). It seems, however, that population sizes in the epilimnion are generally much larger than in the hypolimnion. Kyle and Noblet (1986, 1987) investigated the vertical distribution of thermotolerant naked amoebae and found highest abundances in the upper surface microlayer, high abundance in the surface layer and lower abundances deeper in the water column of a pond and a lake. Increases in the abundance of amoebae were observed at strata of high light attenuation. Much more information is available regarding the vertical distribution of the testacean genus *Difflugia*. When abundant in plankton, highest concentrations were found in the epilimnion. In the upper surface layer of an old sand pit low abundances were recorded, and maxima occurred in 1 m depth (Meisterfeld, 1991, Fig. 4B). Abundances decreased with increasing depth. In addition, the percentage of empty tests and inactive organisms increased towards the anoxic hypolimnion.

Relative contribution of planktonic sarcodines to zooplankton biomass

The decision to include planktonic sarcodines in a plankton study requires some estimation on the relative contribution of sarcodines. Despite of the scarcity of available data sets, one general conclusion may be drawn from section 4C: whenever microbial activities on particles will be studied, naked amoebae have to be considered as potential inhabitants. Another conclusion from a view on the results of several authors (Figs. 4 and 5) is obvious: the contribution of sarcodines is very variable. Sarcodine biomass in Lake Müggelsee ranged from 0 to 55 per cent of the total protozooplankton biomass. *Difflugia* may, at times, contribute up to 61 per cent of combined ciliate and testacean biomass in Lake Oglethorpe (Pace, 1982), and considering other protozooplankters (*cf.* Bennett *et al.*, 1990) also a considerable proportion of total protozooplankton biomass. In the highly productive, tropical Lake Valencia, Venezuela, "amoeboid forms" composed 6 per cent of the annual average

biovolume of protozooplankton (Lewis, 1985). There are lakes, probably rare, where *Difflugia* can dominate total zooplankton biomass (*e.g.* Nelson and Harp, 1972).

At present, a clear trend regarding the influence of lake trophy on the relative contribution of sarcodines to the protozooplankton is not evident. When comparing data for a mesotrophic (Mathes, 1992) and for a highly eutrophic lake (Arndt *et al.*, 1993), sarcodines composed a relatively similar part to total annual mean protozooplankton biomass (mesotrophic Neumühler See: 2.3%, eutrophic lake Müggelsee: 1988: 15.5, 1989: 2.6, and 1990: 1.1%, *cf.* Fig. 5B and C). In 25 north German lakes of a trophy ranging from oligo/mesotrophic to hypertrophic, sarcodines were very variable in their contribution (Mathes, pers. comm., Arndt and Mathes, 1991). Considering aggregates as a possibly important substrate, this is not surprising (see above). The total abundance and biomass of sarcodines, however, seem to increase significantly with an increase in trophy (*cf.* Table II). The same has been documented for total heterotrophic nanoplankton by Berninger *et al.* (1991).

If the biomass of planktonic sarcodines is compared with that of the total zooplankton, including metazoans, a reduction in the importance of sarcodines results (Lake Neumühler See: 0.45% of the annual mean biomass of zooplankton was due to sarcodines; Lake Müggelsee: 1988: 3.10%, 1989: 0.46%, and 1990: 0.12% resp., Mathes and Arndt, unpubl.). Even considering the much higher metabolic rates of the very small sarcodines compared to that of metazoans, sarcodines are probably not of importance in annual averages of whole lake metabolism, but, at least regarding their short-term occurrence, their patchy distribution, and their selective feeding impact, sarcodines should be significant (see below).

Food and activity of planktonic sarcodines in lakes

Studies on the feeding ecology of limnetic sarcodines in the planktonic habitat are rare. However, since pelagic and benthic forms may be closely related (sometimes the same species may occur), some general conclusions may be drawn from benthically oriented studies. Sandon (1932) gave a comprehensive overview regarding the feeding ecology of sarcodines. Limnetic sarcodines may be bacterivores (*e.g.* small amoebae), algivores (amoebae, heliozoans), carnivores (heliozoans, amoebae); mixotrophs may occur at least among amoebae and heliozoans (*cf.* Christopher and Patterson, 1983; Patterson and Dürrschmidt, 1987; Sanders, 1991). Even metazoans have been reported as a food source of heliozoans (*e.g.* Hollowday, 1949). Many sarcodines may be omnivorous, others seem to be selective feeders (*cf.* Schaeffer, 1917; Sandon, 1932). Even very small heliozoans (20 μm) were observed to be voracious predators on large ciliates (*e.g.* Wetzel, 1926). Bacterivorous amoebae can be selective regarding the efficient use of certain bacterial strains (*cf.* Frosch, 1897; Sandon, 1932). The same was observed for algivorous species (Ho and Alexander, 1974; Wright *et al.*, 1981; Laybourn-Parry *et al.*, 1987). It is generally believed that small amoebae are bacterivorous, however this view has to be reconsidered, since small forms (< 15 μm)

have also been observed to be algivorous (*e.g.* Yamamoto and Suzuki, 1984). An apparently untested assumption is that floating amoebae are not able to feed. It seems more likely that floating stages indicate phases of searching for food (*e.g.* suitable substrates and food particles). In chemostats with a continuous supply of small *Cryptomonas* sp. floating stages of an undetermined naked amoebae (inoculated from plankton samples of Lake Mondsee, Austria) grazed efficiently on heterotrophic and autotrophic flagellates as indicated by live-observations (Arndt, unpubl.).

Most planktonic sarcodines that occur in freshwater reproduce by simple binary fission, though occasionally several daughter cells have been observed to originate from one single cell (Cook *et al.*, 1974). According to the relationship between generation time and cell volume determined by Baldock *et al.* (1980, temperature range 8.5-20°C) the reproductive potential of naked amoebae may be calculated. For the prevailing size range in plankton habitats from 5 to 20 µm a generation time from 4 to 15 hours can be computed. Generation times obtained for a small brackish water heliozoon lie in the same range (Tobiesen, 1991). That means most planktonic sarcodines would be able at least to double their biomass every day. During *in situ* incubations of unfiltered lake water (1l-bottles) of Lake Müggelsee the community of suspended naked amoebae showed doubling times of 0.74 to 1.70 per day (mean 1.17 ± 0.47; 5 experiments from April to October 1988, Arndt unpubl.). Mortality due to predation by zooplankters was not considered in these experiments. The obtained rates of increase indicate that naked amoebae may be able to reach the potential growth rate in the field. The possible impact of planktonic sarcodines on plankton populations may roughly be evaluated assuming that about one third of assimilated carbon of food particles is transferred into sarcodine body carbon. This would mean that sarcodines doubling their biomass once per day would need to consume about three times their body weight per day.

Considering a grazing impact on the plankton community that may be three times their own biomass, the impact of planktonic sarcodines on plankton communities may be at least occasionally of importance, especially, when selective feeding is considered. Field observations of sudden appearance and disappearance of planktonic sarcodines (amoebae) in the plankton of lakes connected with a complete destruction of algal blooms (Canter and Lund, 1968; Cook *et al.*, 1974; Hayashi *et al.*, 1989) are clear indications for the potential impact that planktonic sarcodines may have to structure the plankton community of lakes. Cook *et al.* (1974) reported that one large mayorellid-like amoebae could ingest and disrupt trichomes of *Anabaena* of more than 20 cells in less than 2 minutes.

Little is known regarding the impact of planktonic sarcodines on bacteria and other picoplankters. It is very likely, that the impact of bacterivorous amoebae is concentrated on picoplankters associated to particles. A rough estimation of the grazing pressure of naked amoebae using the example of Lake Müggelsee, Berlin, may be given. The annual mean biomass of naked amoebae (bacterivorous species prevailed) was about 30 µg fresh weight per liter in 1989 and 3.5 µg in 1990, resp. The bacterial production for these two years ranged between 0.2 and 839 mg C m^{-2} d^{-1} (Nixdorf and Arndt, 1993). If one would accept several assumptions to estimate the grazing impact by naked

amoebae (dry weight is 20% of fresh weight; 45% of dry weight is carbon; feeding rate is 3 times their body carbon; 80% of the community feeds on bacteria on particles) and assume further that 20% of bacterial production is produced on particles (this seems to be an overestimation for Lake Müggelsee, Nixdorf, 1990 and pers. comm.) then about 90% of the bacterial production on particles would be consumed by amoebae in 1989 and about 20% in 1990. In addition, omnivorous amoebae may feed on other protozoans (heterotrophic nanoflagellates, ciliates), algae or detrital particles on the aggregates. Naked amoebae may contribute significantly to the degradation of detrital carbon in Lake Müggelsee. During 1988 at the extremely high abundances of naked amoebae (*cf.* Fig. 2), their impact should have been even more pronounced. This very rough estimation indicates that on annual average, too, the activity of sarcodines cannot be neglected, if their selective impact is considered.

The impact of heliozoans is more difficult to estimate owing to their probably more omnivorous feeding behaviour. During peak abundance of carnivorous/ omnivorous heliozoans, these sarcodines can have a significant impact on autotrophic and heterotrophic flagellates and probably also on ciliates.

Preliminary thoughts on the role of sarcodines in the pelagic microbial food web

In Figure 6 an attempt was made to summarize the present knowledge regarding the trophic position of sarcodines in lake plankton. The broken lines indicate the ability of sarcodines to change their habitat. This opportunity may vary from species to species. In addition, transport of cysts is another important mechanism of distribution which is not considered in the figure.

Planktonic sarcodines are generally not as abundant as heterotrophic nanoflagellates, but may be as abundant or even more abundant than ciliates (*cf.* Table II). Although, sarcodine occurrence is more sporadic than that of ciliates. The information regarding the quantitative aspect of trophic relationships is very limited. Those relationships which have been described in literature are shown in Figure 6 as a continuous arrow. Trophic relationships which are very probable, but for which I did not find support in literature, are indicated by a question mark. Additional relationships may be probable, but have to be investigated in future.

As indicated in the previous section, the grazing impact of sarcodines on algae and bacteria cannot be ignored when analyzing the pelagic matter flux. At least for short periods sarcodines may be of importance. The fate of planktonic sarcodine production has been analysed semiquantitatively by Schönborn (1962a) for a population of *Difflugia*. During the decline of the planktonic population in autumn he observed that a significant number of individuals have died in their tests, some had formed cysts and others survived the winter living as benthic organisms. These, in addition to predation, may be the major loss factors of planktonic sarcodines. Schönborn (1992) showed in a recent review that the daily mortality of shelled sarcodines lies in the range of 5-10% per day. Cook *et al.* (1974) observed a massive disintegration of naked amoebae after
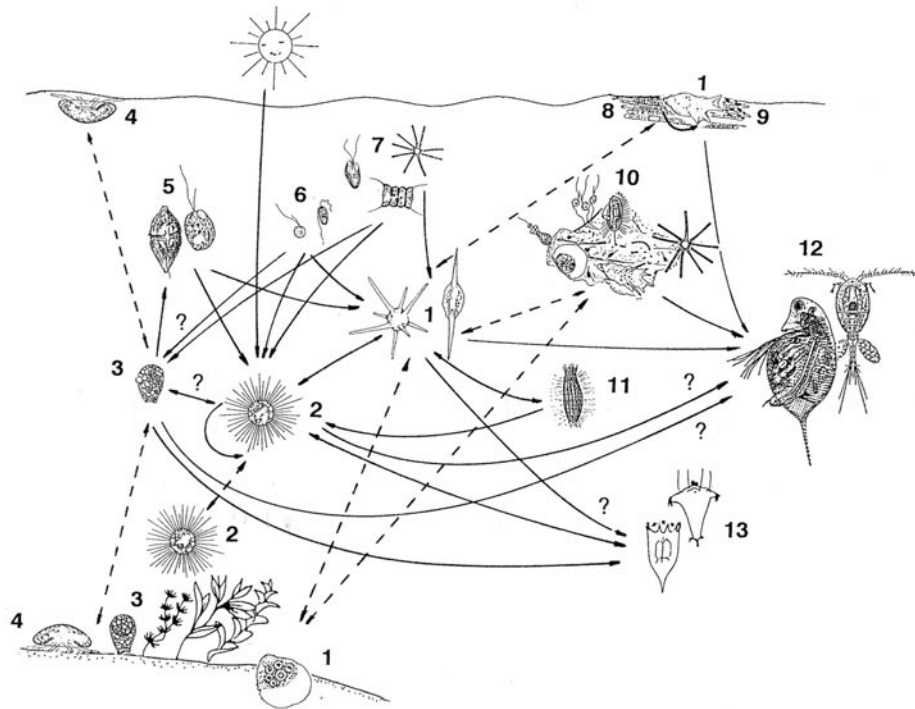
Fig. 6. Attempt to characterize the position of sarcodines in the plankton community of a lake. Broken lines indicate changes in the habitat. Continuous lines indicate trophic relationships. 1: naked amoebae; 2: heliozoans; 3 and 4: testaceans; 5: large heterotrophic flagellates; 6: heterotrophic nanoflagellates; 7: phytoplankton; 8: blue-green filaments; 9: attached bacteria; 10: detrital floc; 11: ciliates; 12: meso-metazooplankton; 13: micro-metazooplankton.

mass occurrence during a bloom of cyanobacteria. Quantitative data on losses due to predation have seldom been reported. A review of literature (*cf.* Sandon, 1932) indicates that large heterotrophic flagellates, sarcodines themselves and ciliates could be potential predators. Koste (1978) reported on rotifers that feed on heliozoans and testaceans. It may be that metazoan filter-feeders consume all small planktonic sarcodines. However, whether stickiness or association to particles may protect sarcodines from being consumed, has still to be investigated. The quantity of fluxes between organisms of the same species living in the planktonic habitat and those living in the benthic (or epiphytic) habitat is not well-studied. Probably, a simultaneous action of all three factors — excystment/encystment, changing buoyancy, rapid population growth — may cause rapid changes in the abundance of sarcodines in plankton. These outbursts have shown to cause rapid and severe effects on the plankton community. Ignoring these short-term peaks of activity will lead to an incorrect understanding of the pelagic matter flux regarding the fate of algae and most probably that of picoplankton and protozoans on particles. Future studies require more detailed investigations regarding the taxonomic composition of planktonic sarcodines.

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