



Geographic variability in amoeboid protists and other microbial groups in the water column of the lower Hudson River Estuary (New York, USA)



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ABSTRACT

In comparison to other groups of planktonic microorganisms, relatively little is known about the role of amoeboid protists (amebas) in planktonic ecosystems. This study describes the first geographic survey of the abundance and biomass of amebas in an estuarine water column. Samples collected in the lower Hudson River Estuary were used to investigate relationships between ameba abundance and biomass and hydrographic variables (temperature, salinity, and turbidity), water depth (surface and near bottom), distance from mid-channel to shore, phytoplankton biomass (chlorophyll fluorescence) and the occurrence of other heterotrophic microbial groups (heterotrophic bacteria, nanoflagellates, and ciliates) in the plankton. Although salinity increased significantly towards the mouth of the estuary, there were no significant differences in the abundance or biomass of any microbial group in surface samples collected at three stations separated by 44 km along the estuary's mid-channel. Peak biomass values for all microbial groups were found at the station closest to shore, however, cross-channel trends in microbial abundance and biomass were not statistically significant. Although ameba abundance and biomass in most samples were low compared to other microbial groups, clear patterns in ameba distribution were nevertheless found. Unlike other microbial groups examined, ameba numbers and biomass greatly increased in near bottom water compared to surface samples. Ameba abundance and biomass (in surface samples) were also strongly related to increasing turbidity. The different relationships of ameba abundance and biomass with turbidity suggest a rising contribution of large amebas in microbial communities of the Hudson estuary when turbidity increases. These results, emphasizing the importance of particle concentration as attachment and feeding surfaces for amebas, will help identify the environmental conditions when amebas are most likely to contribute significantly to estuarine bacterivory and C-flux.

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1. Introduction

Amoeboid protists are single-celled eukaryotes characterized by amoeboid motion and the presence of one or more locomotory pseudopods (Page, 1983, 1988). This is a functional and morphological definition, representing many groups of organisms that are not necessarily closely related. Here, we will use the term 'ameba' specifically to mean naked (non-testate), amoeboid protists, and our focus is free-living amebas, more typically found in aquatic environments, exclusive of the "slime molds" and their relatives.

Amebas are considered the most important group of bacterial grazers in soils (e.g., Clarholm, 1981; Bonkowski, 2004; Anderson,

2012). In contrast, although ubiquitous in aquatic environments, amebas are often thought of as having only a minor role in planktonic ecological fluxes because their natural abundance is thought to be low compared to other heterotrophic protists, such as ciliates and nanoflagellates (e.g., Laybourn-Parry, 1992; Strom, 2000). While natural ameba abundance in the water column is often observed to be comparatively low, there have been numerous reports of high abundance and biomass (summarized in Lesen et al., 2010). For example, Murzov and Caron (1996) found high abundances of naked amebas in Black Sea plankton, peaking at 4×10^5 cells l^{-1} , when amebas dominated the biomass of heterotrophic nanoplankton ($<20 \mu m$). Other studies have also occasionally found planktonic ameba abundances as high as 10^5 – 10^6 cells l^{-1} in diverse near-shore environments (Anderson, 1997; Rogerson and Gwaltney, 2000; Rogerson and Hauer, 2002; Anderson, 2007). However, ameba abundance in offshore waters

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generally appears to be much lower; Davis et al. (1978) reported finding only 0.4 l^{-1} in subsurface water sampled from the North Atlantic. The localized abundance of amoebas in particulates may nevertheless be high, even in the open ocean. For example, high amoeba abundances were noted in association with pelagic *Trichodesmium* colonies in the Sargasso Sea (Anderson, 1997). Similarly, Caron et al. (1982) reported concentrations of planktonic protists (including amoebas) in Sargasso Sea macroaggregates (marine snow, *Trichodesmium* tufts, and *Rhizosolenia* mats) that were four orders of magnitude greater than in samples of the surrounding water. Nonetheless, research on the distribution, abundance and biomass of naked amoebas in open ocean and coastal waters is much less prevalent than research on other planktonic protists.

The relative rareness of such reports may be partly related to methodological biases. Amoebas are usually destroyed by commonly-used field collection and preservation methods, and they are difficult to visualize and identify microscopically. Genomic tools have been used to track particular amoeba species of interest (e.g., Mullen et al., 2005). However, the taxonomic diversity of amoebas is too broad, and the sequence database remains too sparse, to currently apply genomic techniques to detect and enumerate all amoebas in field samples (Nikolaev et al., 2004, 2006; Smirnov et al., 2011). Therefore, amoebas must currently be enumerated separately from other planktonic microorganisms using specialized and labor-intensive, direct microscopic observational methods (e.g., Anderson and Rogerson, 1995).

Given the relatively sparse data on planktonic amoebas in estuarine waters, Lesen et al. (2010) documented the temporal variability in abundance and biomass of amoebas at a single, near-shore location in the Hudson River Estuary (HRE) in relation to other major groups of heterotrophic protists in the water column at that site. Mean amoeba biomass exceeded that of ciliates, but was more variable than ciliate or heterotrophic nanoflagellate biomasses. Earlier work had also found that amoeba biomass within the HRE, and in some highly productive freshwater habitats, often exceeded that of ciliates (Anderson, 2007). While in-situ growth and bacterivory rates for amoebas are difficult to quantify, available evidence suggested that mean rates for amoebas were comparable to those of other heterotrophic protists (Lesen et al., 2010), consistent with prior reports of surface grazing rates of some marine benthic amoebas (e.g., Rogerson et al., 1996). Thus, at times when amoeba biomass is a significant fraction of the total for heterotrophic protists, they likely contribute significantly to total bacterivory, phytoplankton grazing, and carbon fluxes. Nevertheless, amoeba abundance and biomass seem to be characterized by much higher spatial and temporal variability than other heterotrophic protists in the plankton (Murzov and Caron, 1996; Lesen et al., 2010).

Given sporadic high amoeba biomass coupled to high variability in estuarine environments, understanding the factors driving variability in planktonic amoeba biomass would be valuable. In particular, predicting the conditions that most favor high amoeba biomass would help in determining when the extra effort to enumerate this group would be most useful. In the few temperate locations that have been studied, amoeba biomass varied seasonally, with peaks occurring in spring and summer (Anderson and Rogerson, 1995; Lesen et al., 2010), possibly related to more suitable temperatures for growth. Lower abundance and activity in colder conditions, as during winter in temperate regions, is consistent with observations from Antarctic waters (Mayes et al., 1997, 1998).

Because amoebas attach to, move, and feed on surfaces (Pickup et al., 2007), they are associated with particles (Rogerson et al., 2003) and it is likely that particle characteristics are a major determinant of their abundance and biomass. For example, mean size, carbon biomass, and the diversity of amoeba morphospecies

increase with increasing particle size (Anderson, 2011), and high amoeba abundance has been found in aquatic environments with high particulate load, such as ponds and mangroves (Rogerson et al., 2003; Anderson, 2007). Similarly, Murzov and Caron (1996) noted that the highest amoeba counts in the Black Sea were from locations with abundant water-column particulates. However, quantitative relationships between amoeba abundance and biomass with turbidity, or other direct estimates of particle load, have not been derived for any aquatic ecosystem.

In this study, amoeba concentrations and biomass were estimated in multiple locations within the HRE. The objectives were to assess whether amoeba abundance and biomass varied in relation to: 1) the estuarine salinity gradient; 2) water depth; 3) hydrographic variables such as temperature, salinity, and turbidity; and 4) other planktonic microbial groups within the estuary. In general, we hypothesized finding significant relationships between heterotrophic protists (including amoebas) and their likely prey, heterotrophic bacteria or phytoplankton. With respect to amoebas, given observations of high amoeba abundance and biomass in water columns with high particle load (Murzov and Caron, 1996; Rogerson et al., 2003; Anderson, 2007) we hypothesized that amoeba abundance and biomass would increase with turbidity. In addition, also due to their particle-associated lifestyle, we hypothesized finding higher amoeba abundance near the bottom, compared to surface water samples.

2. Materials and methods

2.1. Sample collection and location

Surface water samples were collected at 5 locations within the salinity-stratified portion of the lower HRE on three dates: September 24, 2008, October 20, 2008, and May 12, 2009. This portion of the estuary has high particulate load from suspended sediments. In general, phytoplankton production in the HRE is strongly light limited due to high turbidity and vertical mixing, and by short residence time (Cole and Caraco, 2006; Howarth et al., 2006; Landeck-Miller and St. John, 2006). Surface station locations were chosen to allow several specific comparisons. Three mid-channel stations (1, 2, and 3, Fig. 1A) were chosen to provide data on potential trends along the estuarine salinity gradient. Northernmost station 1, in the Tappan Zee region of the estuary, is always the freshest of the three, while station 3, near the southern tip of Manhattan Island, is the most saline. Stations 1 and 3 are separated by approximately 44 km.

Station 1, together with two additional stations 4 and 5, represent a mid-channel to near shore transect (Fig. 1B). Data from these three stations were used to study potential cross channel trends. Station 5 has been the focus of several previous investigations of microbial abundance and activity in the HRE (Anderson and Rogerson, 1995; Anderson, 2007; Lesen et al., 2010). In addition to the surface sampling, on several dates, near bottom water samples were collected at mid-channel stations 1 and 2. These data were used to examine potential trends with depth.

Samples from near-shore station 5 were collected by wading out from shore to where water depth was approximately 0.5 m (3–4 m from the shoreline). All other samples were collected from the Riverkeeper survey vessel, R. Ian Fletcher (www.riverkeeper.org). For each surface sample, an autoclaved 250-ml polypropylene bottle was held several cm below the water surface until it was full. On four occasions, when we sampled a mid-channel station at the surface, we also collected a near bottom sample (from within the bottom meter). Three of these near bottom samples came from station 2, one from station 1. For near-bottom samples, a 250-ml sample bottle was filled from a 2.5-l Niskin bottle (General

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