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First Limnological Characterization of the Tropical Crater Lake Amparihibe in the Makira Protected Area, Madagascar

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Abstract

The newly established Makira Protected Area and its environs in Northeast Madagascar host roughly 50% of the entire Malagasy floral biodiversity, but very little was known about the two freshwater lakes found within the park. Lake Amparihibe was explored for the first time in November 2007. According to preliminary 40Ar/39Ar dating, the volcanic crater formed as far back as 25.3 million years ago, but no information is available about when the crater started to fill with water. The protected crater lake has a maximum depth of 28 m and was anoxic beyond a depth of 15 m. During the single sampling occasion, steep gradients in temperature, oxygen, conductivity and pH revealed a stable stratification. Several phyto- and zooplankton taxa showed distinct depth-specific abundance maxima along the steep physico-chemical gradients. The majority of plankton organisms have a cosmopolitan (tropical and temperate) distribution, however more taxonomic research is necessary before definitive conclusions can be drawn. Exposure of a multi-mesh gill net together with visual inspection by snorkeling yielded no presence of fish. Despite the full protection status of the park, illegal introduction of alien fish species seems a realistic threat to this pristine Malagasy lake.

Profile

Protected area

Makira Protected Area

Mountain range

Ampokafobe Plateau

Country

Madagascar

Introduction

The island of Madagascar has been separated from the African mainland for about 165 million years (Rabinowitz et al. 1983), and it has been isolated from all other land masses, most recently from India, for approximately 90 million years (Raval & Veeraswamy 2003). Due to this long isolation a unique fauna and flora has evolved, characterized by high levels of endemism. Hence biologists often refer to the fourth largest island of the world as an island continent (Tyson 2000). Surveys of aquatic organisms depicted Madagascar as a global hotspot of freshwater biodiversity (Groombridge & Jenkins 1998). Since the 1990s the number of newly described species of aquatic insects and fish has increased exponentially (Benstead et al. 2003). It is still a matter of debate, however, whether endemic species also developed in planktonic organisms. Whereas some authors state that there is indisputable evidence of endemisms and restricted geographical distributions (e.g. Dumont 1983), Fenchel and Finlay (2004) argue that all organisms with cysts < 1 mm should easily be dispersed across barriers such as the Mozambique channel and potentially be cosmopolitan. This contrasts with the views of other authors on phytoplankton taxa, for which group-specific endemism is assumed. In Madagascar this has been documented especially for chrysophytes (Hansen 1996; Kristiansen & Lind 2005), diatoms (Metzeltin & Lange-Bertalot 2002) and desmids (West & West 1895; Bourelly & Couté 1991). Biogeographic regions of phytoplankton taxa are becoming more and more evident (e.g. Coesel 2002). However, in contrast to benthic habitats, the number of biogeographically restricted tropical and tropical-warm temperate phytoplankton taxa usually make up only a small proportion (not more than 10-20%) of the overall richness of tropical lakes (see Rott et al. 2008; Schabetsberger et al. 2004).

Surveys of the Malagasy freshwater algal flora from various habitats are quite patchy (West & West 1895; Fritsch 1914; Manguin 1941; Bourrely & Leboime 1946; Bourrelly & Manguin 1949). More recent algological investigations are available for mostly non-planktonic desmids (Bourrelly & Couté 1991; Coesel 2002), chrysophytes (Hansen 1996) and benthic diatoms from subaerial (Spaulding & Kociolek 1998a, b) and benthic freshwater habitats (Metzeltin & Lange-Bertalot 2002). Taxonomic research on micrometazoa

Lake Amparihibe © Gabriele Drozdowski

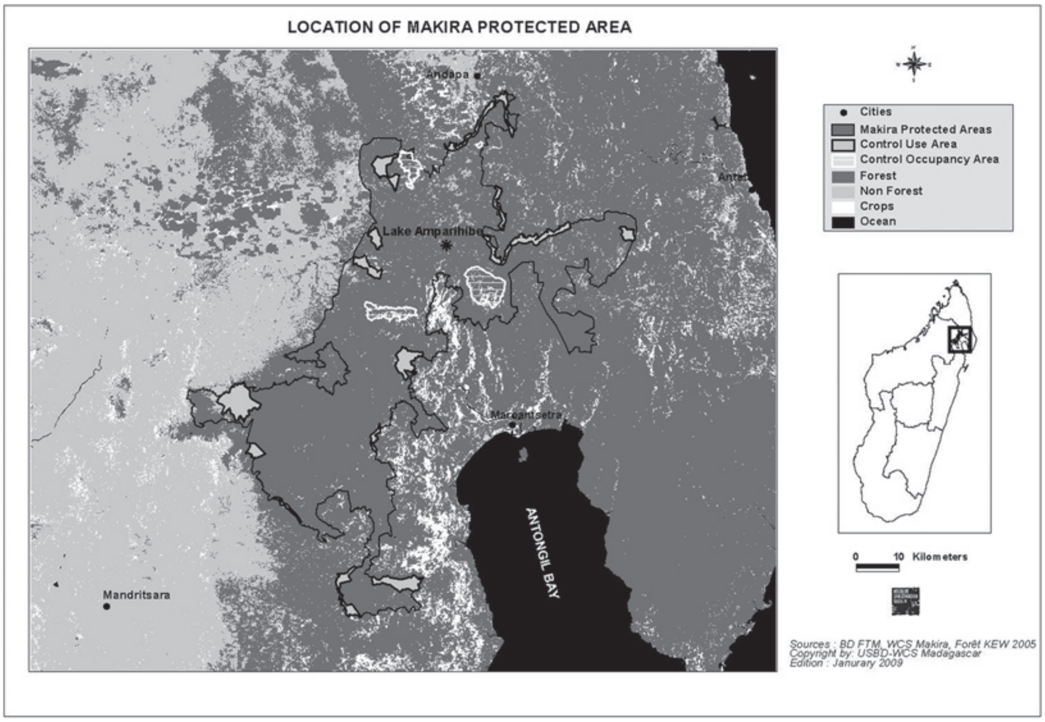

Figure 1 – Map of the Antongil Bay area in NE Madagascar showing the Masoala National Park and the Makira Protected Area. Control use area: natural resources can be harvested by local people for their living; Control occupancy area: controlled settlement of local people possible.

was conducted predominantly until the 1960s and is also fragmentary (De Guerne & Richard 1893; Brehm 1930; 1948; Kiefer 1930). Most studies were based on samples taken by the director of the "Institut des recherches scientifiques de Madagascar", Renauld Paulian, who sent the material to various taxonomists (Rotifera: Berzins 1960; 1973; 1982; Harpacticoida: Chappuis 1952; 1954; 1956; Calanoida: Brehm 1951; 1952 a, b, c; 1953; 1954; Cyclopoida: Lindberg 1951 a, b; 1952; 1953; Kiefer 1952; 1954; 1955; Cladocera: Brehm 1953). Brehm (1960) gave an account on freshwater crustacea collected during the Austrian Madagascar expedition in 1958. Few publications appeared after this peak period of taxonomic work on freshwater micrometazoa (Dussart 1982; Segers 1992; Fiers 2002). Although much more remains to be done, endemic algae (e.g. Metzeltin & Lange-Bertalot 2003; Coesel 2002), rotifers (Berzins 1982), and copepods (Dussart 1982) have been discovered in Malagasy freshwater ecosystems. Dumont (1983) even called the comparatively large number of 18 endemic rotifers the "Madegassian anomaly"; however Berzin's (1960) description of the endemic genus *Repauliana* probably was a misidentified preservation artefact of *Tetrasiphon hydrochora* (W. Koste personal communication). Nevertheless a systematic survey of Malagasy lakes would contribute substantially to the question of endemic versus cosmopolitan distribution in freshwater planktonic organisms.
Systematic species inventories of pristine lakes must be started before the last natural communities may be destroyed. With a loss of 40% of rainforest cover between 1950 and 2000 (Harper et al. 2007), Madagascar anticipates the fate of tropical rainforest habitats worldwide. If deforestation of the eastern rainforest continues at the rate of 1.6% per year (102 000 ha), only the steepest slopes will remain forested by 2025 (Green & Sussman 1990). Deforestation causes increased sediment delivery and nutrient input into the lakes and hence alters physico-chemical conditions, species composition and trophic interactions (Benstead et al. 2003). In addition, alien fish species such as tilapias may be stocked once logging and slash-and-burn agriculture closes in on the lakes. These introduced fish usually cause severe changes to the entire ecosystem (Schabetsberger et al. 2009). Very likely the species communities within lakes near human settlements have long been altered. Hence Benstead et al. (2003) define three major objectives to conserve the remaining freshwater biodiversity: (1) Survey efforts have to be directed at remote regions that have not been inventoried for freshwater biota. (2) Systematic and ecological studies of poorly known taxonomic groups must be undertaken. (3) Top conservation priority should be given to intact freshwater ecosystems that are situated within protected areas. So far only few lake ecosystems in Madagascar have been investigated (see Moreau 1988 and references therein) and even fewer pristine lakes remain within the rainforests of Madagascar. Some isolated crater lakes are found in the mountainous regions of Northern Madagascar. Lake Amparihibe ("The big lake") and the considerably smaller Lake Lohanimanandriana are the only lentic water bodies within the Makira Protected Area. This newly established protected area is

among the largest remaining contiguous areas of tropical rain forest in Madagascar and as part of the larger Antongil Bay landscape harbours roughly 50% of the floral biodiversity found in Madagascar (Wildlife Conservation Society 2008a). Hence, the aim of this study was a first limnological characterization of Lake Amparihibe, with the focus on a survey of phyto- and zooplankton species and estimates of their densities.

Materials and methods

Study site

The Makira Protected Area covers 371 456 hectares of rainforest between 50 m and 1 200 m elevation. Mean annual temperatures range from 22.5 to 25.8°C, but may drop below 15°C at Lake Amparihibe. Annual rainfall in the area varies between 1 100 and 3 500 mm and exceeds 180 days. It decreases during the southern winter (April to November), from East to West, and towards higher altitudes. During the summer the trade winds from the East decrease and are counterbalanced by monsoon winds from the North. The frequency of cyclones hitting the area during this rainy season increased during the last decade (one in 2000 and 2004 and two in 2007; Wildlife Conservation Society 2008b). The park contains seventeen rivers and two lakes. Lake Amparihibe, situated at an altitude of 798 m (15° 2.275'S, 49° 35.057'E; Figure 1), was reached after a one days journey by boat (52 km) on the river Antainambalana and a three days march (43 km) through the rainforest. The volcanic crater lake is surrounded by intact eastern rainforest, has a diameter of 430 m and a maximum depth of 28 m. The approximately 60 m deep crater from rim to water surface has an inclination of 50% and more. Numerous little creeks flow into the lake, which has one large outflow in the West that falls over a ca. 5 m high cascade.

40Ar/39Ar dating

Using the 40Ar/39Ar method, whole-rock or mineral samples can be dated by determining the ratio of radiogenic 40Ar to neutron-induced 39Ar. An in-situ volcanic rock sample was collected on the northern shore of Lake Amparihibe (15° 2.207'S; 49° 34.963'E) and analysed at the Department of Geology of the University of Salzburg. A detailed description of the methodology can be found in Rieser et al. (2007).

Limnology

Water samples were taken in the central part of the lake from an anchored dinghy. In the afternoon of November 12, 2007, water temperature, oxygen concentration and saturation, conductivity and pH were measured with portable devices (Hanna Instruments) at 0, 5, 7.5, 10, 12.5, 15, 20 and 25 m depth. On November 13, 2007, two series of zooplankton samples were collected with a 4.5 l Schindler-Patalas trap at 0, 2.5, 5, 10, 15, 20, and 25 m depth, filtered through a 30 µm mesh and preserved in 4% formaldehyde. Additionally, phytoplankton samples (100 ml) were collected at 0, 5, 10 and 15 m depth and preserved with Lugol's iodine. In the laboratory, zooplankton samples were stained with Rosé Bengal. Phytoplankton analyses followed Rott's (1981) recommendations for counting and biovolume calculations using the Utermöhl technique. For phytoplankton species identifications a larger set of literature relevant also to tropical environments was used (e.g. Komarek & Fott 1983; Rott et al. 2008). The entire zooplankton sample was counted under an inverted microscope.
A standardized multimesh gill net was exposed overnight from the shoreline outwards to the lake centre (30 m length, 1.5 m width; 12 mesh sizes: 5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43, 55 mm). Additionally, we snorkelled around the shoreline and screened the littoral habitats for the presence of fish.

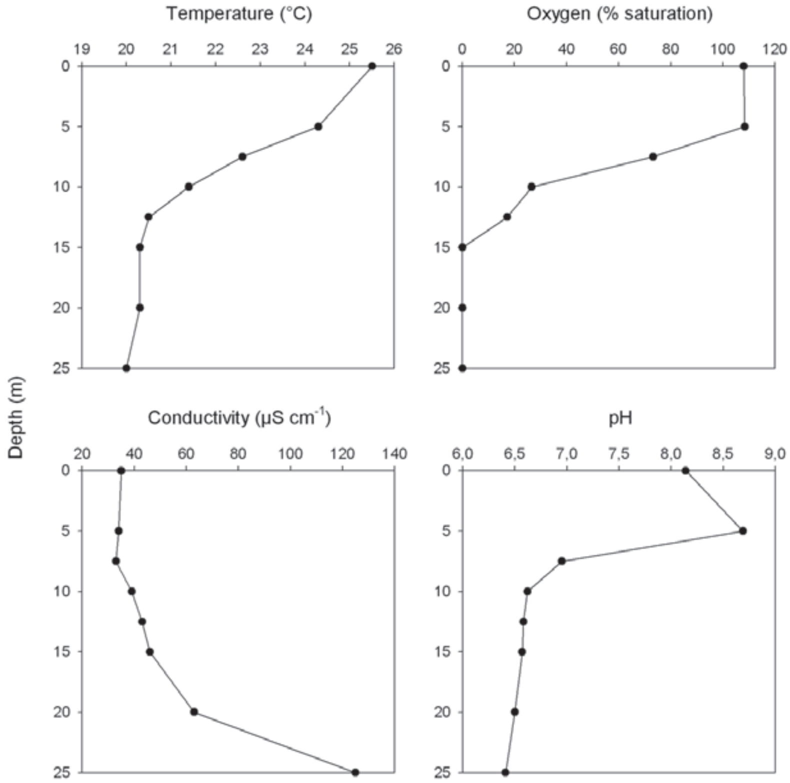

Figure 2 – Temperature, oxygen, conductivity, and pH gradients of Lake Amparihibe on November 12, 2007.

Results

40Ar/39Ar dating

The dated volcanic rock yielded an isochron age of 25.3 ± 1.2 Ma (initial 40Ar/39Ar = 299 ± 9).

Abiotic parameters

The water body of the protected crater lake was stratified: Temperature dropped from 25.5°C at the surface to 21.4°C at 10 m depth and reached 20.0°C above the sediment (Figure 2). Correspondingly, a strong oxycline was observed between 5 (128% saturation) and 10 m (27%). Beyond 15 m the hypolimnion was anoxic and conductivity increased from 43 to 125 µS

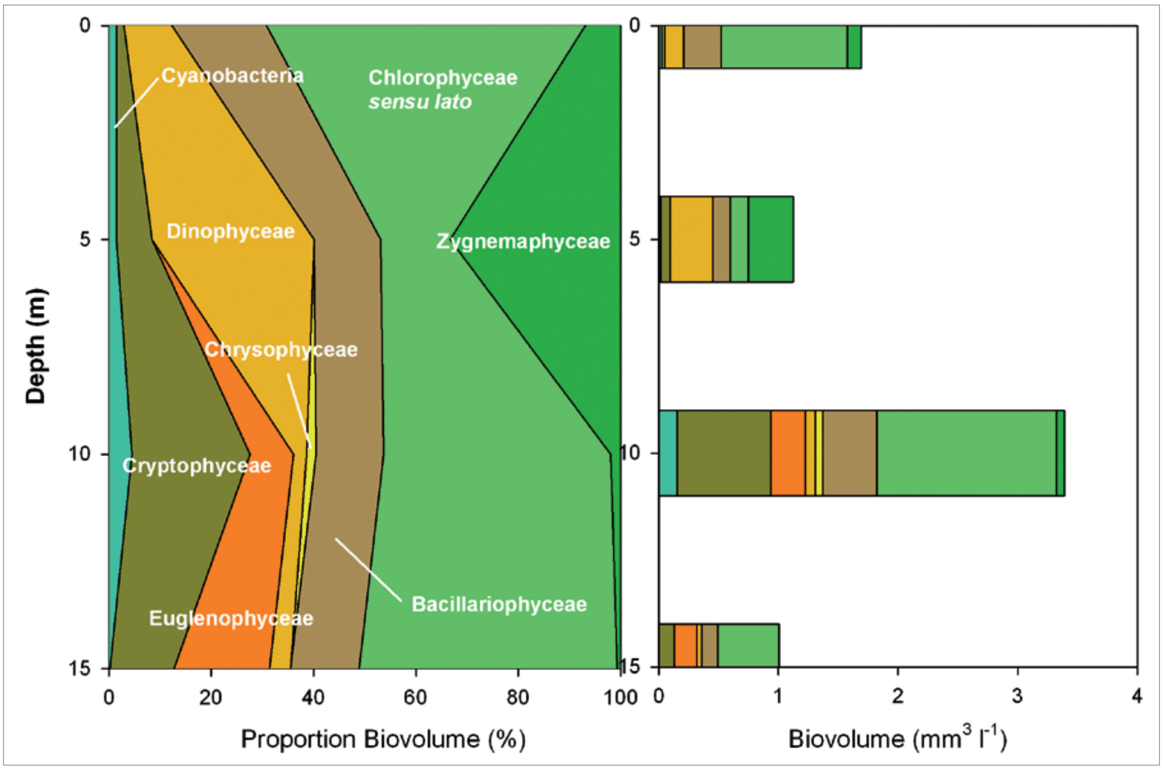

Figure 3 – Vertical distribution of the different groups of algae in Lake Amparihibe, shown as relative proportion of biovolume (left) and absolute biovolume (right).

cm^{-1} in 25 m, thereby increasing stability of the water body. The pH increased from 8.1 to 8.7 in the top five meters and then dropped to 6.4 above ground. The oversaturation with oxygen and increased pH-values in the top layers were related to peak abundances of small desmids (see below).

Phytoplankton

A total of approximately 42 taxa were recorded including a few characteristic African taxa (e.g. *Cylindrospermopsis africana, Peridinium africanum*), but so far no new species were discovered (Table 1). In terms of biovolume, Chlorophyceae dominated the phytoplankton with mostly minute single-celled taxa (e.g. *Chlorella, Monoraphidium, Nephrochlamys*), except for subsurface layers around 5 m depth, where Zygenmaphyceae (three or more minute *Cosmarium*-like taxa < 10 µm, with high shape variability for which preliminary names are listed in Table 1) and Dinophyceae prevailed (Figure 3). Euglenophyceae and Cyanobacteria reached highest abundance at low oxygen conditions around 15 m depth. Overall algal biomass was highest in layers below pH and oxygen maxima.

Zooplankton

Seven species of rotifers dominated the zooplankton community in the oxygenated layers (Table 1). They exhibited a clear depth segregation (Figure 4), with *Polyarthra vulgaris* dominating at the surface, *Hexarthra intermedia* at 2.5 m, and the *Trichocerca* species at 5 m, whereas *Anuraeopsis fissa* reached its highest abundance together with a gastrotrich species (*Neogossea* cf. *antennigera*) within the chemocline. Early cyclopoid copepodites and *Chaoborus* cf. *ceratopogones* larvae were most abundant in shallow subsurface layers. A maximum of the ciliate *Pelatractus* sp. was found at the upper boundary layer of the hypolimnion.

Fish

No fish were seen or caught. Nevertheless the presence of eels (*Anguilla* spp.) cannot be excluded.

Discussion

The 40Ar/39Ar dating showed that the crater of Lake Amparihibe probably formed during the Tertiary and hence is much older than the numerous craters in the large volacanic complex of the Montagne d'Ambre north of the Makira Protected Area (Schleicher 2009). Since the major focus of this study was a limnological characterization of the lake, the age estimate from a single rock sample has to be treated as a preliminary result. Nor do we have any information when the crater filled with water to become a permanent lake, because no sediment cores were taken. Nevertheless these first results show that Lake Amparihibe is one of the few old freshwater ecosystems far from any human settlement and is therefore particularly interesting for the investigation of pristine freshwater species assemblages in Madagascar.

The clear stratification of Lake Amparihibe and its protected position within the crater suggests that it remains stratified throughout the year or at least for long periods, although more sampling, especially after cyclones have hit the lake, would be required to confirm a permanent anoxic hypolimnion. During our sampling, only the top 15 m of the open water, together with a relatively narrow belt of benthic habitat, could be colonized by aerobic organisms. Concordantly, most planktonic species exhibited clear depth-specific maxima in abundance. Different dominant taxa of both phyto- and zooplankton were found in the different layers of the epilimnion (desmids, dinoflagellates, most rotifers), the oxycline (*Cryptomonas* spp., Cyanobacteria, Gastrotricha, *Anuraeopsis fissa*), and the upper layers of the anoxic hypolimnion (*Trachelomonas* sp., *Pelatractus* sp.; Figures 3 + 4).

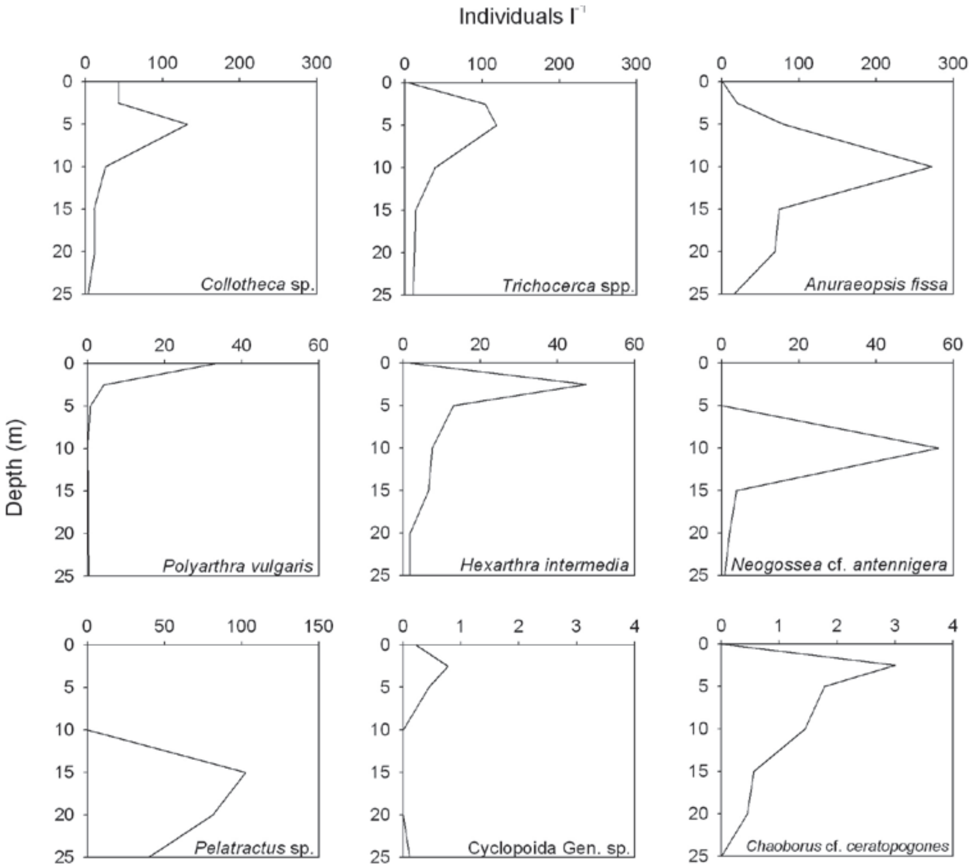

Figure 4 – Vertical distribution of the dominant zooplankton taxa in Lake Amparihibe.

Nevertheless we found aerobic phyto- and zooplankton organisms in complete anoxia that did not show any signs of deterioration. Several authors report algae, rotifers and crustaceans in extremely hypoxic or oxygen-free waters (Green et al. 1973; Kizito et al. 1993; Kizito & Nauwerck 1995). In a previous study we encountered undamaged phyto- and zooplankton organisms in complete darkness and anoxia at 82 m depth within the crater lake Loreto on Bioko Island, Equatorial Guinea (Schabetsberger et al. 2004). The reasons are probably passive downward transport processes such as sedimentation or entrapment within cooler water masses.

The presence of a considerable portion of mid-sized diatoms throughout the water column (including *Fragilaria crotonensis* and *Ulnaria acus*) indicates that the lake may overturn during certain periods of the year. On the other hand, the presence of the potentially bloom-forming colonial Cyanobacterium *Microcystis aeruginosa* in 10 m depth, below the pH and oxygen maxima, may be indicative for the sedimentation of algal cells from a preceding bloom during warmer periods of the year.

Some phyto- and zooplankton organisms could only be determined to genus or even higher taxonomic level, but among those taken to species level by morphological analyses, we did not discover any new or endemic taxa within this remote crater lake. The rarest species we detected was the rotifer *Trichocerca agnatha*, which so far has only been recorded from the type locality in Germany (Wulfert 1939), from Australia (Koste & Shiel 1980), and from a crater lake on the Malagasy island of Nosy Be (Segers 1992).

Further detailed taxonomic research is required here and for other pristine lake ecosystems of Madagascar to understand better if endemic freshwater plankton organisms developed on the island continent. In this preliminary study of Lake Amparihibe, species with a wide distribution prevailed. Accordingly, in the extremely isolated lakes on South Pacific Islands endemics were only encountered within the Crustacea (Schabetsberger et al. 2009). However, the sole cyclopoid copepod in the lake could not be identified, as it was only present as early copepodites. Yet it remains a matter of debate if the propagules of smaller phyto- and zooplankton organisms are readily distributed by wind, rain or water birds (Bilton et al. 2001; Bohonak et al. 2003). In the future, standard alpha-taxonomy backed by genetic analysis of e.g. cryptic species (Mann & Droop 1996) will help to solve this complex question.

Fish probably never colonized the lake, since they were neither caught in the multimesh gill net nor observed while snorkelling. The outflow of the lake falls over a cascade that forms an insurmountable obstacle for migrating fish. We cannot exclude the presence of eels (*Anguilla* spp.), that are known to crawl over wet soil during heavy rains and may remain hidden during daylight.

Lake Amparihibe remains surrounded by intact low altitude eastern forest and is situated well within the limits of the strict protection zone of the Makira Protected Area. However, we believe that stocking with fish poses a realistic threat to the lake. At least 24 alien

Table 1 – Phyto- and zooplankton species found in Lake Amparihibe, Madagascar

PHYTOPLANKTON
Cyanobacteria
Anabaena sp.
Cylindrospermopsis africana J. Komárek & H. Kling 1991
Planktolyngbya limnetica (Lemmermann) J. Komárková-Legnerová & G. Cronberg 1992
Microcystis aeruginosa (Kützing) Kützing 1846
Merismopedia tenuissima Lemmermann 1898
Oscillatoria sp.
Cryptophyceae
Cryptomonas spp. (20 µm, 27 µm)
Euglenophyceae
Trachelomonas cf. *abrupta* Svirenko 1914
Trachelomonas cf. *volvocina* Ehrenberg 1833
Dinophyceae
Gymnodinium spp. (15 µm, 30 µm)
Peridiniopsis elpatiewskyi (Osternfeld) Bourrelly 1968
Peridinium africanum Lemmermann 1907
Peridinium spp.
Chrysophyceae
Chrysoflagellate unidentified (8 µm)
Bacillariophyceae
Asterionella formosa Hassall 1850
Aulacoseira granulata (Ehrenberg) Simonsen 1979
Cyclotella meneghiniana Kützing 1844
Cyclotella sp. (5 µm)
Fragilaria crotonensis Kitton 1869
Synedra spp. (40 µm, 70µm)
Ulnaria acus (Kützing) M. Aboal 2003
Urosolenia cf. *pusilla* Rott & Kling 2006
Chlorophyceae
Ankistrodesmus cf. *falcatus* (Corda) Ralfs 1848
Botryococcus sp.
Chlorella sp.
Coelastrum proboscideum Bohlin in Wittrock & Nordstedt 1896
Crucigenia tetrapedia (Kirchner) W. West & G.S. West 1902
Dictyopshaerium sp. (3 µm)
Franceia cf. polychaeta (Širšov) Korshikov 1953

PHYTOPLANKTON
Micractinium cf. *pusillum* Fresenius 1858
Monoraphidium contortum (Thuret) Komàrková-Legnerová 1969
Monoraphidium sp.
Nephrochlamys sp. ad *N. subsolitaria* (G.S. West) Korshikov 1953
Tetraedron minimum (A. Braun) Hansgirg 1888 forma!
Treubaria triappendiculata C. Bernard 1908
Volvocales undidentiefied (8 µm)
Zygnemaphyceae
Closterium sp. (40 µm)
Cosmarium cf. *pusillum* (Brébisson) W. Archer 1861
Cosmarium cf. *regnesii* Reinsch 1867
Cosmarium cf. *subcapitulum* West & West f. *minor* Taylor 1934
Mougeotia sp.
Staurastrum sp.

ZOOPLANKTON
Protozoa
Pelatractus sp.
Urotricha sp.
Rotifera
Anuraeopsis fissa Gosse 1851
Collotheca sp.
Hexarthra intermedia Wiszniewski 1929
Polyarthra vulgaris Carlin 1943
Trichocerca agnatha Wulfert 1939
Trichocerca pusilla Lauterborn 1898
Trichocerca ruttneri Donner 1953
Gastrotricha
Neogossea cf. *antennigera* Gosse 1851
Copepoda Cyclopoida
unidentified copepodites
Chaoboridae
Chaoborus (Sayomyia) cf. *ceratopogones* Theobald 1903

species have been introduced into Madagascar's lakes and rivers (Benstead et al. 2003 and references therein). Tilapias (*Oreochromis* spp., *Tilapia* spp., *Sarotherodon* spp.) are readily available, handy to transport and would serve as an easy to catch source of protein. Due to size-selective predation, fish would irreversibly change both species composition and abundance of the natural community. In remote crater lakes on South Pacific Islands we found reduced species richness in stocked versus unstocked lakes (Schabetsberger et al. 2009).

In the particular case of Lake Amparihibe the threat of stocking could most likely originate from out-of-control movements of local inhabitants through the forests. It is important to note that a population of more than 150 000 inhabitants resides in the border forest landscape of the protected area. An additional threat is represented by illegal harvesting of hardwoods from within the park. Encampments near the lake could invite introduction of fish into the lake.

The Madagascar Ministry of Environment, Forests and Tourism has delegated the management authority of the Makira Protected Area to the Wildlife Conservation Society. The Society is currently engaged in a program of community forest resource management. Principal components of this program are education and awareness campaigns to improve community land stewardship. Such information campaigns and continuous controls by park field agents are necessary to keep the lake fishfree. In addition, more efforts should be made to survey and study the few remaining pristine lakes in Madagascar. Continued ecological and taxonomic research in combination with better management strategies is vital to safeguard their biodiversity.

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Two anonymous reviewers critically read the manuscript and provided helpful comments. We are indebted to Rupert Lenzenweger (Zygnemaphyceae), Wilhelm Foissner (Ciliata), Christian Jersabek (Rotifera), Maria Balsamo (Gastrotricha) and Rüdiger Wagner (Chaoboridae) for species identification. Johann Genser helped with the age determination of the rock sample. We thank Aristide Andrianarimisa and Noromalala Raminosoa for logistic support and Jacky Andriantiana, Petra and Bernd Stolle, Gunter Fischer and the many porters from the villages of Ambinanitelo und Sahantaha for help during field work. Hanitra Rakoto produced the map. This research was conducted under permit 0240/07 issued by the Ministère de l'Environment, des Eaux et Forets, Madagascar.


Lake Amparihibe © Gabriele Drozdowski

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