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Limnological characterization of volcanic crater lakes on Uvea Island (Wallis and Futuna, South Pacific)

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Abstract

Species composition and vertical distribution of planktonic organisms in Lakes Lalolalo, Lanutavake, and Lano on the Pacific Island Uvea were investigated in relation to the physico-chemical water column profiles of temperature, conductivity, dissolved oxygen, and pH. The meromictic lakes Lalolalo (maximum depth: 88.5 m) and Lanutavake (23.6 m) exhibited a strong chemocline with anoxic conditions below 10 m depth. Mixis was inhibited by sheltered topography, thermal stratification, and in Lalolalo a strong halocline. While crustaceans and rotifers were limited to the oxygenated epilimnion, the diversity and density of ciliates were highest within and below the chemocline. In Lalolalo, euryhaline rotifers dominated the community, reflecting the brackish condition of the lake. Species richness and densities were highest within the shallow lake Lano (3.5 m). On a calm day, hypoxic conditions occurred near the sediment-water interface but higher oxygen concentrations were observed after heavy winds indicating occasional mixis. In total, 32 phytoplankton species, 23 ciliate taxa, 18 rotiferan, 1 cladoceran, 1 copepod, and 1 gastrotrich species were identified in the pelagic zones of all three lakes.

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Introduction

The crater lakes on volcanic South Pacific islands are among the most isolated lentic freshwater ecosystems on Earth. All freshwater animals and plants arrived through long distance dispersal via rain, wind, birds or humans (reviewed in Kristiansen 1996, Bilton et al. 2001, Bohonak and Jenkins 2003, Havel and Shurin 2004, Panov et al. 2004, Green and Figuerola 2005, Vanschoenwinkel et al. 2008) making these lakes targets for studies of dispersal abilities and biogeography (Schabetsberger et al. 2009).

Brief descriptions of the many lakes and wetlands throughout Oceania have been published (Dahl 1980, Scott 1993), but a limited number of detailed limnological studies have been conducted (Maciolek and Yamada 1981, Southern et al. 1986, Schabetsberger et al. 2009 and references therein). To our knowledge, depth-specific samples to study physico-chemical profiles have only been collected in four lakes: Lake Letas (Gaua, Vanuatu; Baker 1929), Vai Lahi (Niuafo'ou, Tonga; Maciolek and Yamada 1981), Tagimaucia crater lake (Taveuni, Fiji; Southern et al. 1986), and Lake Kauhakō (Molokai'i, Hawai'i; Donachie et al. 1999).

Uvea, or Wallis Island (Wallis and Futuna, France) harbors seven lakes (Figure 1), but only preliminary surveys of freshwater organisms are available (Mary et al. 2006, Schabetsberger et al. 2009). Hydrological studies to evaluate freshwater resources on Uvea Island have been conducted recently (Comte 2012*a*,*b*, Irz et al. 2012).

The objective of this study was to link depth-specific distribution of phytoplankton, ciliates and planktonic micrometazoa to physico-chemical profiles of Lakes Lalolalo, Lanutavake, and Lano. The study complements the first palaeolimnological coring in the remote crater lakes of Uvea Island (Maloney et al. in prep.).

Materials and Methods

Study area

Uvea is the main island of the French overseas territory Wallis and Futuna in Western Polynesia. It is of volcanic origin and is surrounded by a barrier reef with 22 islets. The central island (59 km^2, highest point Mt. Lulu 151 m) has seven crater and depression lakes (Figure 1). Due to the high permeability of the rocks, no surface streams exist (Stearns 1945). The mean annual air temperature is 27 °C with small seasonal amplitude (±1 °C). The mean annual precipitation amounts to 3 m, most of which falls during the rainy season from October to May (Meisch et al. 2007, Irz et al. 2012). The volcanic island of Uvea probably rose from the sea during the Tertiary and the three lakes investigated in this study Lalolalo, Lanutavake, and Lano (Figure 2, Table 1) were created by phreatomagmatic explosions during the late Holocene (Stearns 1945). The basins of the other lakes Lanutuli, Lanumaha, and Alofivai were probably created earlier during the mid-Pleistocene.

<<Fig. 1 near here>>

Lake Lalolalo (S 13° 18.050, W 176° 14.052; Figure 2a, Table 1) is the largest and deepest lake on the island. The view from the crater rim with its spectacular 50 m vertical cliffs surrounding the circular lake is one of the major attractions for the few tourists reaching Uvea, but the lake itself is relatively undisturbed by humans due to the difficult access and the “vao tapu”, an ancient, traditional law that protects the lake and the circumjacent forest (Guiot 1998). The only native fish species in Lake Lalolalo is the Pacific shortfinned eel (*Anguilla obscura)*. It is hypothesized that the eels enter the lake through an underwater connection to the ocean (Mary et al. 2006). Lake Lanutavake (S 13° 19.287, W 176° 12.846; Figure 2b, Table 1) has less steep slopes than Lalolalo on its crater rim, is surrounded by dense vegetation and easier to access.

Although it lacks infrastructure, Lanutavake is frequently utilized for leisure activities by the local population. Lake Lano (S 13° 17.650, W 176° 14.429; Figure 2c, Table 1) is surrounded by marshes and dense vegetation making access to the water difficult and resulting in little human disturbance. Due to the surrounding topography, Lake Lano is less wind sheltered than the other two lakes. Tilapia (*Oreochromis mossambicus*) was introduced into Lalolalo and Lanutavake in 1966 (Hinds 1969) and probably transferred from there to Lano. Today tilapia occurs in large numbers in all three lakes (Mary et al. 2006, Schabetsberger et al. 2009, personal observations). According to Mary et al. (2006) and Morat and Veillon (1985), no submerged aquatic angiosperm vegetation exists in any of the three lakes.

<<Table1 near here>>

<<Fig. 2 near here>>

Physico-chemical depth profiles

Sampling was conducted between 11:00 a.m. and 4:00 p.m. from 10 to 21 May 2011. Temperature, conductivity, dissolved oxygen, and pH were measured with a submersible multi-parameter sonde (Hydrolab Quanta). Sampling depths and schemes are shown in Table 2. In Lalolalo and Lanutavake three, in Lano two replicate water column profiles were measured on different days and average values were calculated. For depths greater than 25 m in Lalolalo, water was collected with a 5 L Schindler trap and measured with the data sonde immediately after sampling. Depth recordings were done with an echo sounder (Norcross Hawkeye Digital Sonar DF 2200PX). Maximum depth in Lalolalo, exceeding the range of the echo sounder, was determined by using a line and a weight.

Plankton organisms

Phytoplankton, ciliates, and micrometazoa were sampled between noon and 5:00 p.m. with a 5 L Schindler trap above the deepest points of the lakes (Table 2).

Phytoplankton

Phytoplankton samples (50 ml) were preserved with acetic Lugol's solution. In the laboratory, phytoplankton was concentrated through centrifugation and analyzed qualitatively. Light microscopic investigations from subsamples were done under an Olympus BX 50 and a Motic BA 400 microscope with objectives 40 and 100x (oil immersion), both equipped with phase contrast. Cell walls were stained with Gentian Violet and Methylene Blue, and starch was colored with Lugol's solution (Ettl and Gärtner 1995).

Ciliates

For qualitative ciliate analyses, approx. 1-2 L per sample were filtered through a 10 µm plankton net and for quantitative analyses, unfiltered samples (50 ml) were taken. All samples were preserved with acetic Lugol's solution or 75 % ethanol and stained with protargol (quantitatively after Skibbe 1994, qualitatively after Vd'ačný and Foissner 2012). Ciliates were observed by using an Olympus BX51 microscope and identified from literature keys (Foissner et al. 1999 and references therein). The permanent slides were deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI) and are publicly available. Lugol-preserved ciliates were not stained well with protargol, nevertheless, the different taxa could be well separated from each other.

Micrometazoa

5 L per sample were filtered through a 30 µm net and fixed with 4% formaldehyde. In the laboratory, organisms were stained with Bengal Rose for at least 24 h. Copepods, cladocerans and large rotifers were counted under a stereo microscope at 25 x magnification, while smaller

rotifers were counted with a Nikon Eclipse TS 100 inverted microscope using the sedimentation method after Utermöhl (1958).

<<Table2 near here>>

Results

Physico-chemical depth profiles

Lalolalo

Steep physico-chemical gradients were observed (Figure 3a). A distinct chemocline was found around 10 m depth with oxygen steeply declining from 6.4 mg L^{-1} (88 % saturation) at the surface to 1.2 mg L^{-1} (17 %) at 9.5 m, and anoxic conditions in 10.5 m depth. Concurrently, temperature decreased from 31.7 °C at the surface to 30.6 °C at 9.5 m depth and then dropped to 27.1° C at 20 m. The lake also exhibited a strong halocline. At the surface the water was at the threshold of fresh- to brackish conditions (1.7 mS cm^{-1}; 0.86 PSS). Conductivity steeply rose below 50 m depth from 7.3 to 48 mS cm^{-1}, corresponding to a salinity of 31.3 PSS, near that of sea water. The pH at the surface was well above neutral (8.5), but quickly dropped to slightly acidic conditions (6.8) in the monimolimnion.

Lanutavake

Similar to Lalolalo, a chemocline existed around 10 m depth with anoxic conditions below. Temperature profiles in both lakes were similar within the mixolimnion, but at 22.5 m Lalolalo was 2 °C colder than Lanutavake (Figure 3b). Conductivity remained below 200 µS cm^{-1} at the deepest point. The pH dropped from 8.4 to 7.0 between the surface and 9 m and reached a minimum of 6.3 at maximum depth.

Lano

Temperature decreased from 32.0 °C at the top to 30.2 °C at the bottom (Figure 3c). Oxygen dropped from supersaturated conditions (7.9 mg L^{-1}, 108% saturation) at the surface to almost anoxic conditions at the sediment water interface (0.2 mg L^{-1}, 3%). A weak gradient in conductivity from 36 to 90 µS cm^{-1} was observed along the water column. The pH dropped from 7.3 at the surface to 5.8 at the sediment-water interface. After a windy day, higher oxygen concentrations were observed in deeper layers indicating mixis of the entire water column.

<<Fig. 3 near here>>

Plankton organisms

A total of 32 phytoplankton species, 23 ciliate taxa, 18 rotiferan, 1 cladoceran, 1 copepod, and 1 gastrotrich species were found in the pelagic zone of the three crater lakes (Table 3).

Lake Lalolalo

The phytoplankton community of Lalolalo was the least diverse of all three lakes, with nine species identified. Since most of the taxa from the flagellate genera *Gymnodinium*, *Peridinium*, *Cryptomonas,* and *Chlamydomonas* could not be identified to species level, it is not possible to assess their halotolerance. However, all of the other phytoplankton species are known to be widely distributed among various, mostly freshwater, water bodies. At least five of the nine species found are flagellates with known potential for vertical migration. Only *Chlorella* sp., *Monoraphidium arcuatum*, and *Tetraedron triangulare* are immotile coccal algae.

Nine ciliate taxa were identified at depths of 0-8 m (*Mesodinium* sp., *Cinetochilum* sp., *Vorticella* sp., undetermined Scuticociliatia, Hymenostomatia, Litostomatea and Prostomatea). Within and below the chemocline at depths between 10 and 15 m, the highest ciliate diversity of all lakes investigated was observed, including *Cinetochilum* sp., *Coleps* sp., *Colpodidium/Paracolpidium, Pseudocohnilembus* sp., *Paramecium/Frontonia*, *Vorticella* sp., *Mesodinium* sp., and undetermined species belonging to the Armophorea, Haptorida, Prostomatea, Loxodida, Stichotrichia and Scuticociliatia. With increasing conductivity only one additional species (prostomatid) was detected at 35 m and no ciliates were found at 50 and 80 m depths. Ciliate densities at depths of 0-4 and 15 m were 6.0 and 6.8 ind. mL^{-1}, respectively (Figure 4a).

The zooplankton community of Lalolalo consisted of salt tolerant species and had low species diversities relative to the two freshwater lakes. Euryhaline *Hexarthra brandorffi* and *Epiphanes brachionus* var. *spinosa* dominated the rotiferan community reaching combined maximum densities of almost 100 ind. L^{-1} (Figure 4a). Highest densities of rotifers and of the only copepod *Mesocyclops aspericornis* were observed near the chemocline at 9 and 10 m, respectively. Few micrometazoan specimens (< 5 ind. L^{-1}) were detected in the anoxic monimolimnion below 11 m.

Lake Lanutavake

The phytoplankton community in Lanutavake was more diverse than in Lalolalo. Seven identified species and at least 13 unidentified species of *Peridinium* occurred in the lake. Pyrrhophytes (dinoflagellates) dominated the phytoplankton assemblage, followed by chlorophytes and insignificant appearance of cyanoprokaryotes in the form of single colonies.

Six ciliate taxa occurred at depths of 0-6 m, predominantly *Cinetochilum* sp., *Cyrtolophosis* sp. with algal symbionts, *Halteria/Pelagohalteria,* Scuticociliatia, and single haptorids and prostomatids. Samples from the microaerobic and anaerobic zone revealed additional taxa such as *Coleps* sp., *Holophrya* cf. *discolor, Monodinium* sp., *Pelagolacrymaria/Phialina*, *Urotricha* sp., and not assignable haptorids, prostomatids and scuticociliates. Ciliate density at depths of 0-6 m was 4.1 ind. mL^{-1} (Figure 4b).

Rotifer densities were 10 times higher in Lanutavake than in Lalolalo (Figure 4b). In total, nine species were found with *Anuraeopsis fissa*, *Ascomorpha saltans* and *Polyarthra indica* being the most prominent. The copepod *M. aspericornis* exhibited a more even distribution throughout the mixolimnion with all developmental stages reaching twice as many individuals as found near the chemocline of Lalolalo. Furthermore, the cladoceran *Ceriodaphnia cornuta* complemented the zooplankton community.

A gastrotrich (*Polymerurus* sp.) was found in the anoxic monimolimnion below 13 m depth with highest densities at the deepest sampling depth at 23 m (6.6 ind. L^{-1}).

Lake Lano

In the shallow lake Lano the highest number of phytoplankton species (26) was found. The phytoplankton community was dominated by Chlorophyta (16). All species found are widely distributed and typical for shallow eutrophic waters.

Nine different ciliate taxa were detected (*Cinetochilum* sp., *Cyrtolophosis* sp., *Halteria* cf. *bifurcata, Halteria/Pelagohalteria, Mesodinium* sp., and undetermined haptorids and scuticociliates). *Cyrtolophosis* sp. was not observed in the oxygen-depleted 3 m depth where only single scuticociliates were found. Average ciliate density was 79 ind. mL^{-1} (Figure 4c).

Dominant rotifers in Lano were similar to those found in Lanutavake with the algivorous species *Ascomorpha saltans* reaching densities of more than 2,500 ind. L^{-1} in the surface water. Copepod densities were similar to Lanutavake, but only nauplii and copepodids were found (Figure 4c).

<<Fig. 4 near here>>

Discussion

The two deep crater lakes, Lalolalo (88.5 m) and Lanutavake (23.6 m), exhibited an anoxic hypolimnion and are most likely meromictic. Given the strong physico-chemical stratification of the lakes observed and their sheltered position within the volcanic craters, total mixis is highly unlikely even during heavy storms. Although the shallow lake Lano (3.5 m) also showed anoxic conditions near the sediment-water interface, total mixis probably occurs during heavy rain and wind.

In Lalolalo, a steep increase in salinity occurred at depths around 45 m. It likely results from the crater extending deeper than the Ghyben-Hertzberg freshwater lens of the island followed by an intrusion of seawater by horizontal hydraulic conductivity through the rock or fractures of unknown size between the lake and the sea. Given that the water level was around 1.3 m above sea level (Irz et al. 2012), the theoretical interface between fresh- and saltwater should occur around 55 m depth, which is 10-15 m deeper than the observed steep increase in salinity. However, the relatively high permeability of the geologically young bedrock may facilitate the enhanced intrusion of salt water over the theoretical prediction (Comte 2012*a*,*b*). The deepest points of Lanutavake and Lano lay above this theoretical interface, explaining the absence of salt water intrusions. Ocean tides were found to not have a direct influence on the water surface level of Lalolalo (Irz et al. 2012). Therefore, high salt concentrations could also be remnants from a now-closed fissure. Further studies including ^{14}C-dating of the dissolved inorganic carbon could give an estimation of the age and the origin of the salt (Maloney et al. in prep.). Still, the occurrence of eels in Lalolalo but not in the other two lakes (Mary et al. 2006; personal observations) support the previous assumption of an underwater connection to the ocean, through which elvers could enter the lake. However, there are no data on eel size distribution available to proof constant immigration.

The physico-chemical gradients determined the species richness and the vertical distribution of planktonic organisms. In the two deeper lakes, rotifers and copepods were predominantly restricted to the aerobic epilimnion, while ciliates were thriving at low oxygen conditions close to the chemocline. In Lalolalo rotifer communities were dominated by few euryhaline species due to the brackish condition of the lake. Highest densities of micrometazoa just above the chemocline may indicate rich feeding conditions such as bacteria, algae and detritus for rotifers. The overall lower density of micrometazoa in Lalolalo remains unexplained until more information about bottom up (nutrients) and top down effects (fish predation) is available. The higher phytoplankton and rotifer species richness in Lano could also be explained by the lake's smaller size and depth and hence the larger proportion of littoral and epibenthic organisms in the open water.

Most of the plankton organisms were cosmopolitan or widely distributed species. Presumably, their propagules arrived by wind, rain, birds, or humans. Only the crustaceans were tropical species with restricted distributions, confirming earlier results from South Pacific lakes (Schabetsberger et al. 2009). Nevertheless, it cannot be ruled out that some morpho-species are actually complexes of cryptic species with smaller distribution ranges (Gómez et al. 2002, Fawley et al. 2004, Belyaeva and Taylor 2009). For example, some of the numerous *Peridinium* taxa that could not be determined to species level may be new endemic species. In this respect, the remote lakes on Uvea could harbor genetically isolated lineages of microorganisms (Schröder and Walsh 2007).

The ciliate assemblages detected in the three lakes were distinctly different from previous observations in temperate and tropical lakes (e.g., Beaver and Crisman 1989, Foissner et al. 1999, Ong'ondo et al. 2013, Pfister et al. 2002, Sonntag et al. 2006). The dominating *Mesodinium* species in Lalolalo are widely spread haptorids in pelagic, benthic freshwater and marine habitats. *Mesodinium pulex* has been considered as an indicator species for eutrophic lakes (Edmondson 1910, Beaver and Crisman, 1989, Foissner et al. 1999). The predominance of colpodids or oligohymenophoreans that are known to form cysts may be explained by their higher probability to be transported over long distances (Foissner 2006). As for most euplanktonic ciliate taxa such as small oligotrichs or prostomatids, cyst formation has not been observed so far, an explanation for their absence in these remote lakes could be that they simply could not be transported either atmospherically or by animals. Ciliate numbers observed in Lalolalo and Lanutavake fall in the range of oligo- to mesotrophic lakes, in Lano the density was similar to more productive shallow lakes (Pfister et al. 2002, compilation in Foissner et al. 1999).

The plankton communities likely had changed after the introduction of tilapia. The original intention was the provision of an additional source of protein for the local communities and the biological control of mosquitoes (Mary et al. 2006). But negative impacts on various groups of organisms ranging from plants to birds are often observed after an introduction of the fish (Canonico et al. 2005). However, there are no pre-stocking plankton samples available, and only palaeolimnological studies may shed some light on how the communities changed after tilapias thrived in the lakes.

This study provides a first general depth-specific limnological description of the Uvean crater lakes, showing that two of them are likely meromictic and that the steep physico-chemical gradients determine the species distribution. Abiotic conditions and species communities in surface layers were similar to previous studies conducted during a different season (Mary et al. 2006, Schabetsberger et al. 2009), indicating little seasonal variation. Nevertheless, long-term observations are required to assess the stability of these ecosystems in response to more frequent and intense cyclones predicted from recent climate models (Webster et al. 2005).

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Table 1: Morphometric and limnological characteristics of investigated lakes.

	Lalolalo	Lanutavake	Lano
Altitude [m a.s.l.]	1.3[1]	12.9[2]	3[3]
Max. diameter [m]	480[3]	275[3]	150[3]
Surface area [ha]	15.2[4]	4.6[4]	1.1[4]
Max. depth [m]	88.5	23.6	3.5
Secchi depth [m]	1.7	3.0	unknown

data from [1]Irz et al. (2012), [2]Irz P. pers. communication, [3]estimated following the topographic map of the Institute Geographique National No. 4901, [4]Scott (1993). Other values measured during present study.

Table 2: Sampling depths and schemes in the three lakes. Physico-chemical parameters were either measured with a data sonde *in situ* or within a Schindler trap.

	Lalolalo	**Lanutavake**	**Lano**
Physico-chemical parameters	In situ: 0-12.5 m in 0.5 m intervals 12.5-25 m in 2.5 m intervals, Schindler trap: 30, 35, 40, 50, 60, 70, and 80 m	In situ: 0-14.5 m in 0.5 m intervals, 14.5 – 23.5 m in 1 m intervals	In situ: 0-3 m in 0.5 m intervals
Phytoplankton	0-12 m in 2 m intervals, 35 m all samples pooled	0-12 m in 2 m intervals all samples pooled	0-3 m in 1 m intervals all samples pooled
Ciliates	Qualitative samples: 0, 2, 4 m and 6, 8 m pooled, 10, 12, 15, 35, 50 m Quantitative samples: 0, 2, 4 m pooled, 15, 50, 80 m	Qualitative samples: 0, 2, 4, 6 m, 8, 10, 12 m and 15, 23 m pooled Quantitative samples: 0, 2, 4, 6 m pooled	Qualitative samples: 0, 1, 2, 3 m pooled Quantitative samples: 0, 1 m pooled, 2, 3 m
Micrometazoa	3, 5, 7, 8, 9, 10, 11, 12, 13, 14, 35 m	3, 5, 7, 8, 9, 10, 11, 12, 13, 14, 23 m	0.5, 1, 2, and 3 m

Table 3. List of planktonic organisms found in the three crater lakes and their known global distribution.

Group and Taxa	Site	Distribution
Cyanoprokaryota		
Aphanocapsa sp.	Lanutavake, Lano	
Aphanothece sp.	Lanutavake	
Pyrrhophyta		
Gymnodinium sp.	Lalolalo, Lanutavake, Lano	
Peridinium cf. *africanum* LEMMERMANN, 1907	Lano	cosmopolitan
Peridinium cf. *striolatum* PLAYFAIR, 1919	Lano	Australia
Peridinium spp.	Lalolalo, Lanutavake, Lano	
Cryptophyta		
Cryptomonas obovata SKUJA, 1948	Lalolalo	Europe (North- to temperate)
Cryptomonas sp.	Lalolalo, Lano	
Chlorophyta		
Actinastrum hantzschii LAGERHEIM, 1882	Lano	probably cosmopolitan
Chlamydomonas sp.	Lalolalo	
Chlorella sp.	Lalolalo, Lanutavake, Lano	
Coelastrum pulchrum SCHMIDLE, 1892	Lanautavake, Lano	cosmopolitan
Coelastrum cf. *reticulatum* var. *cubanum* KOMÁREK, 1975	Lanutavake	cosmopolitan (mainly tropical)
Coelastrum cf. *sphaericum* NÄGELI, 1849	Lano	probably cosmopolitan
Didymocystis fina KOMÁREK, 1975	Lano	Cuba, Bulgaria – prob. cosmopolitan
Lagerheimia ciliata (LAGERHEIM) CHODAT, 1895	Lano	probably cosmopolitan
Monoraphidium arcuatum (KORSHIKOV) HINDÁK, 1970	Lalolalo, Lano	cosmopolitan
Monoraphidium komarkovae NYGAARD, 1979	Lano	probably cosmopolitan
Nephrochlamys rotunda KORSHIKOV, 1953	Lano	Europe, Africa?
Pediastrum tetras (EHRENBERG) RALFS, 1845	Lano	Cosmopolitan
Pediastrum tetras var. tetraodon (CORDA) HANSGIRG, 1886	Lano	probably cosmopolitan
Scenedesmus communis (TURPIN)	Lano	probably

HEGEWALD, 1977		cosmopolitan
Scenedesmus magnus MEYEN, 1829	Lano	probably cosmopolitan
Scenedesmus cf. *octocauda* MASJUK, 1962	Lano	N-eastern Europe
Schroederia spiralis (PRINTZ) KORSHIKOV, 1953	Lano	probably cosmopolitan
Tetrastrum heteracanthum var. *homoiacanthum* HUBER-PESTALOZZI, 1929	Lano	probably cosmopolitan
Tetraedron triangulare KORSHIKOV, 1953	Lalolalo	temperate regions (N hemisphere)
Euglenophyta		
Trachelomonas hispida (PERTY) STEIN, 1878	Lalolalo	cosmopolitan
Streptophyta		
Cosmarium sp.	Lanutavake, Lano	
Ochrophyta		
Tetraplektron laevis (BOURRELLY) ETTL, 1977	Lano	temperate Europe
Pseudostaurastrum limneticum (BORGE) CHODAT, 1921	Lano	probably cosmopolitan
Tetraedriella acuta PASCHER, 1930	Lano	Europe, probably cosmopolitan (temperate regions)
Ciliophora		
Armophorea	Lalolalo	
Colpodea (*Cyrtolophosis* sp.)	Lanutavake, Lano	
Litostomatea (Haptoria: *Mesodinium* sp., undet.)	Lalolalo, Lano	
Litostomatea (Haptoria: *Monodinium* sp., *Pelagolacrymaria/Phialina,* undet.)	Lanutavake	
Oligohymenophorea (Scuticociliatia: *Pseudocohnilembus* sp., *Cinetochilum* sp., undet.)	Lalolalo	
Oligohymenophorea (Scuticociliatia: *Cinetochilum* sp., undet.)	Lanutavake, Lano	
Oligohymenophorea (Hymenostomatia: *Paramecium/Frontonia* sp., undet.)	Lalolalo, Lanutavake	
Oligohymenophorea (Hymenostomatia: *Colpidium/Paracolpidium*)	Lanutavake	
Oligohymenophorea (Peritrichia: *Vorticella* sp.)	Lalolalo	
Prostomatea (*Coleps* sp., undet.)	Lalolalo	
Prostomatea (*Coleps* sp., *Holophrya* cf. *discolor, Urotricha* sp., undet.)	Lanutavake	
Spirotrichea (Oligotrichia:	Lanutavake	

Halteria/Pelagohalteria)		
Spirotrichea (Oligotrichia: *Halteria* cf. *bifurcata, Halteria/Pelagohalteria*)	Lano	
Spirotrichea (Stichotrichia)	Lalolalo	
Karyorelictea	Lalolalo	
Rotifera		
Anuraeopsis fissa GOSSE, 1851	Lanutavake, Lano,	cosmopolitan
Ascomorpha saltans saltans BARTSCH, 1870	Lanutavake, Lano	cosmopolitan
Asplanchna brightwelli GOSSE, 1850	Lano	cosmopolitan
Brachionus quadridentatus f. *brevispinus* HERMANN, 1783	Lano	cosmopolitan
Colurella obtusa (GOSSE, 1886)	Lanutavake	cosmopolitan
Epiphanes brachionus var. *spinosa* (ROUSSELET, 1901)	Lalolalo,	pres. cosmopolitan
Filinia cf. *longiseta* (EHRENBERG, 1934)	Lano	cosmopolitan
Hexarthra brandorffi KOSTE, 1977	Lalolalo	Western hemisphere
Keratella quadrata (MÜLLER 1786)	Lalolalo, Lanutavake, Lano	
Lecane closterocerca (SCHMARDA, 1859)	Lanutavake	cosmopolitan
Lecane sp.	Lanutavake, Lano	
Lepadella sp.	Lanutavake	
Polyarthra indica SEGERS & BABU, 1999	Lalolalo, Lanutavake, Lano	Africa, Orient
Synchaeta sp.	Lalolalo	
Trichocerca chattoni (BEAUCHAMP, 1907)	Lano	pres. cosmopolitan
Trichocerca pusilla (JENNINGS, 1903)	Lano	cosmopolitan
Trichocerca tenuior (GOSSE, 1886)	Lanutavake	cosmopolitan
Bdelloidea undet.	Lalolalo	
Copepoda		
Mesocyclops aspericornis (DADAY, 1906)	Lalolalo, Lanutavake, Lano	tropical
Cladocera		
Ceriodaphnia cornuta SARS, 1885	Lanutavake	tropical
Gastrotricha		
Polymerurus sp.	Lanutavake	

Figure 1. Aerial photography of Uvea Island with the capital Mata’Utu and the seven volcanic lakes. © eoVision/U.S. Geological Survey, 2012

Figure 2: Sampling sites on Uvea. Lake Lalolalo (a), Lake Lanutavake (b), and Lake Lano (c).

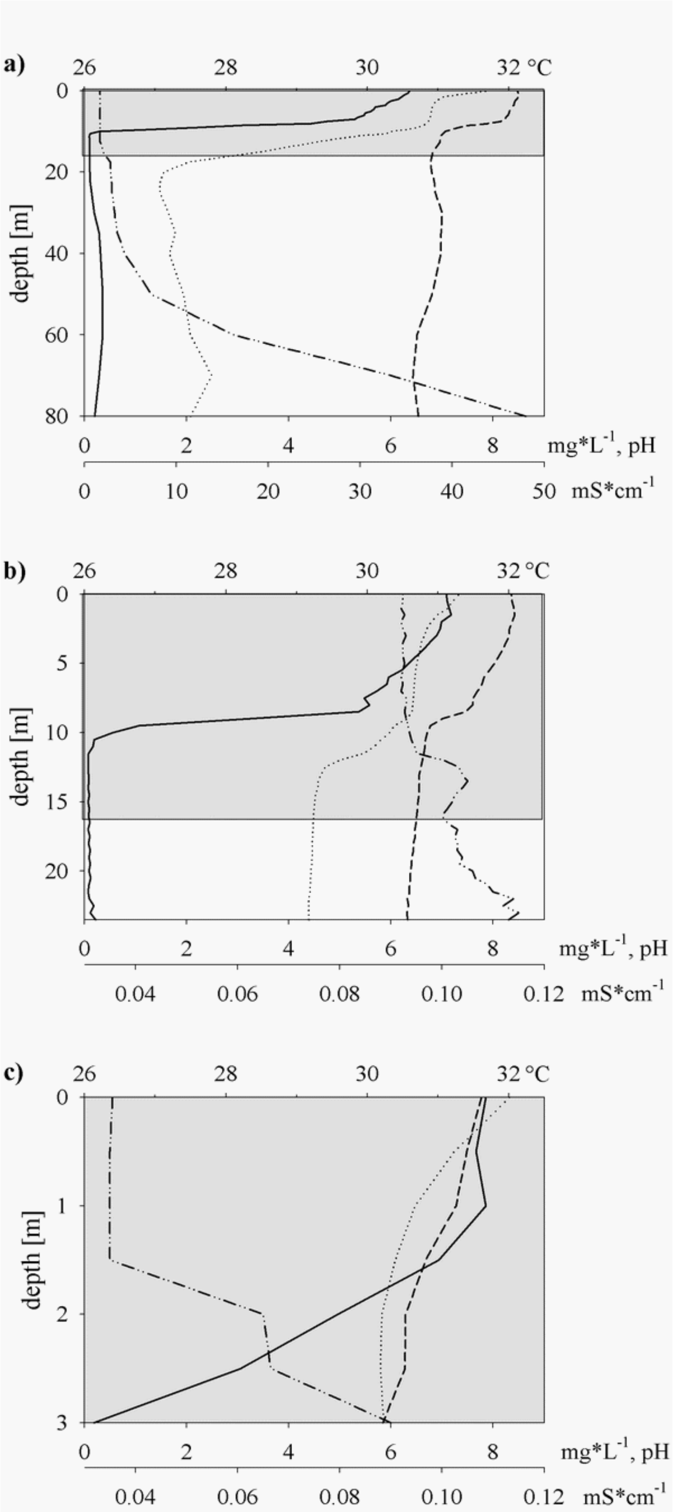

Figure 3: Physico-chemical profiles of Lalolalo (a), Lanutavake (b,) and Lano (c). Temperature [°C] (dotted line), dissolved oxygen [mg L^{-1}] (solid line), pH (dashed line), and conductivity [mS cm^{-1}] (dash-dotted line) are shown. Grey shaded areas mark the water layers included in Figure 4. Note different scales in depths and conductivity.

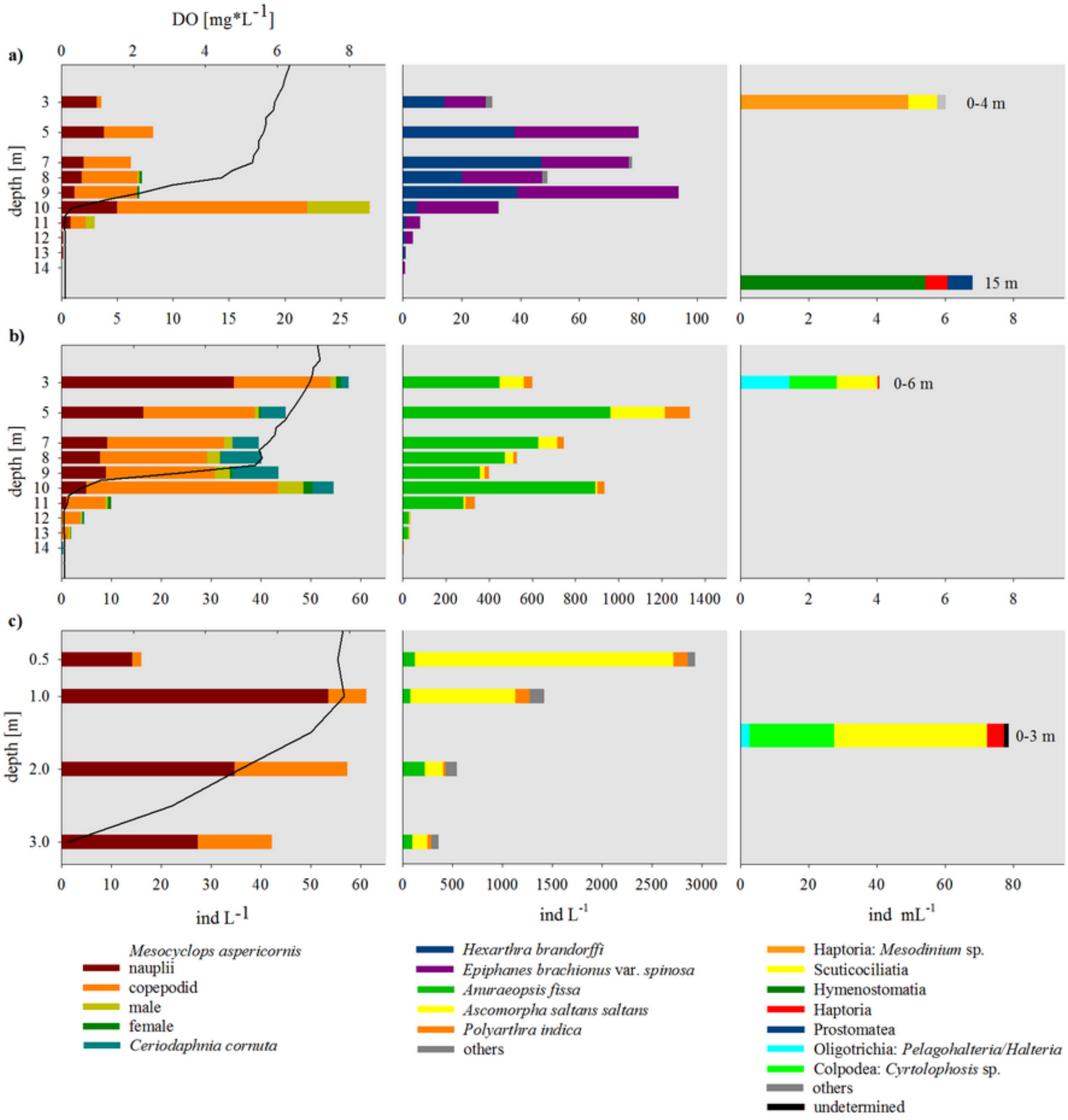

Figure 4. Vertical distribution of planktonic organisms in Lalolalo (a), Lanutavake (b), and Lano (c). Left: Crustacea, Middle: Rotifera, Right: Ciliophora. Solid line represents dissolved oxygen [mg*L^{-1}]. Note different scales in depths and densities.

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