Limnological characterization of the largest freshwater lake in remote Oceania (Lake Letas, Gaua Island, Vanuatu)

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Abstract
With a total area of 19.7 km² Lake Letas (119 m max. depth, 399 m a.s.l.) on Gaua Island, Vanuatu, is one of the largest caldera lakes throughout Oceania. The crescent-shaped lake encircles the active volcano Mount Garet (754 m a.s.l.) whose last major eruption occurred in 2009. In 2012 and 2013, we investigated the lake and its effluent river Mbe Solomul. Physico-chemical depth profiles revealed a thermocline between 10 and 15 m depth. Oxygen dropped gradually from 7.67 mg L⁻¹ at the surface to 0.28 mg L⁻¹ at 95 m depth, indicating occasional holomixis. The inflow of ion-rich water from volcanic springs (913 µS cm⁻¹) lead to relatively high concentrations of SO₄²⁻ (100 mg L⁻¹) and Cl⁻ (60 mg L⁻¹) throughout the water column. Conductivity was highest at the surface (610 µS cm⁻¹), decreased to a minimum of 571 µS cm⁻¹ at 60 m depth, and slightly increased to 576 µS cm⁻¹ above the sediment, probably due to the solution of ions out of volcanic ashes. Surface pH was with 7.8 remarkably lower than measured in 2004 (8.9), possibly as a result of the increased volcanic activity. A Secchi depth of 1.3 m indicated meso- to eutrophic conditions. In contrast, total phosphorous concentration at the surface was with 11.8 µg L⁻¹ relatively low. In total 47 phytoplankton taxa were identified out of which most occurred in the littoral area. The open water was dominated by the filamentous green alga *Planctonema lauterbornii* and the coccoid desmid *Staurastrum depressiceps* var. *gracilis*. The total phytoplankton biomass of 1.06 mg L⁻¹ in the epilimnion reflected the mesotrophic character of the lake. The ciliate assemblage included euplanktonic taxa (*Halteria*, *Mesodinium*, *Coleps*, and *Stentor*) which are commonly detected in temperate and tropical lakes. The zooplankton community was dominated by the copepod *Thermocyclops crassus macrolasius* which reached a maximum abundance of 138 Ind. L⁻¹ at 5 m depth. The littoral was characterized by a dense macrophyte belt consisting predominantly of *Chara australis* and *Ceratophyllum demersum*. The vegetation limit was found at 4.8 m mean depth. Two freshwater eel species *Anguilla megastoma* and *A. marmorata* were the only fish found in the lake, feeding exclusively on macrozooobenthos. In the effluent river the largest *A. obscura* hitherto reported in literature was caught (129 cm), showing that these ecosystems are a habitat of primary importance to Pacific eels.

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Introduction

With a total area of 19.7 km² (Seach 2012) and a maximum depth of 119 m (Thery et al. 1995) Lake Letas is by far the largest lake in remote Oceania (Baker 1929, Scott 1993, Schabetsberger et al. 2009). It lies within the ancient caldera of the still active volcano Mount Garet and is, after the large lakes on the North Island of New Zealand (Timperley and Vigor-Brown 1986) and Lake Wisdom (95 km²) and Lake Dakataua (48 km²) in Papua New Guinea (Larson 1989), the largest caldera lake in the South Pacific.

Until the mid-20th century people settled near the shore of Lake Letas (Joses Togase, Siriti village, Gaua, personal communication). It is not clear if the settlement was abandoned due to WWII turmoil in Melanesia or later, due to increasing volcanic activity. After a long phase of dormancy, Mount Garet became active in 1962. In October 2009 an eruption accompanied by earthquakes, black smoke and ash emission was reported (Geohazards 2009). Forests at the south-western end of the lake were destroyed by toxic emissions (Fig. 1a). Mount Garet is now considered a high risk, permanently active volcano (Seach 2012). With a water volume of 800 million m³ Lake Letas may cause a major phreatomagmatic eruption if the water came in contact with the magma chamber (Németh et al. 2006, Siméoni 2012).

Despite its size, detailed information about the water body is scarce. During a first expedition, Baker (1929) sounded the lake, measured a temperature depth profile, collected a water sample for determination of ion content, and mentioned a few dominant organisms. This author also provided preserved freshwater eels (*Anguilla megastoma, Anguilla osbcura*) for Ege’s (1939) monograph on the Genus *Anguilla*. Thery et al. (1995) drew a first detailed bathymetric map derived from a hydroacoustic survey. Schabetsberger et al. (2009) published a species list of algae and micro-metazoa and confirmed that Lake Letas remains one of the few lakes throughout Oceania not stocked with alien fish species (Eldredge 2000).
An FAO project proposal to protect Lake Letas and its outflowing river as a World Heritage Site is currently under review (FAO 2012). These ecosystems provide a uniquely productive and undisturbed habitat for freshwater eels (Schabetsberger et al. 2009). The caldera is covered by primary rain forest and harbors high species diversity including 19 endemic plant species (Donna Kalfatak, personal observation.)

To provide baseline information for future conservation efforts, depth-profiles of physico-chemical parameters were measured and planktonic organisms, macrophytes, and freshwater eels were studied.

**Materials and Methods**

*Study area*

Gaua Island, also called Santa Maria, (Banks Group, Vanuatu) is the emerged top of an approximately 3,000 m high and 40 km wide basaltic-to-andesitic stratovolcano with a 6 × 9 km large summit caldera. The symmetrical cone of 25 km maximum diameter at sea level is truncated between 500 and 690 m altitude by an 8.5 × 6 km central caldera (Siméoni 2012). Its active volcano Mount Garet (754 m a.s.l., 350 m high, base 3 km) towers over the crescent-shaped Lake Letas (7 × 2 km, 399 m a.s.l., (following the Map of Gaua, Vanuatu, 1416707 X721 Edition 1-VDLS, 2003)). Today, the area around the lake is uninhabited and rarely visited by the local population. It can only be reached by foot after a steep climb of approximately three hours. The only effluent river Mbe Solomul falls over a 120 m high cascade (Siri Falls) and bifurcates into one large (18 m³ s⁻¹) and two small rivers (0.9 and 6.1 m³ s⁻¹) before entering the sea 6 km aerial distance away from the outlet (Fig. 2). During the rainy season the outflow may increase at least twofold (Schabetsberger et al. 2013). Weather stations in Sola, around 40 km north of Gaua
Island, show an average annual precipitation of around 4,000 mm with March being the wettest month (Vanuatu Meteorological Services 2007).

Physico-chemical depth profiles

Lake Letas was visited during two consecutive years in 2012 (19-24 January) before, and again in 2013 (23 March-7 April) at the end of the main rainy season. The difference in the hydro period was not intentionally timed but was a result of logistic circumstances.

In 2012, water samples were taken on 20 January from 10:25 am until 2:00 pm at 14° 16.733’ S, 167° 32.575’ E. An anchor was set and in 2012 all consecutive sampling was done at this position with a maximum depth of exactly 100 m. 1.5 L of water were sampled consecutively with a Schindler- Patalas-trap from 0-95 m in 5 m intervals. Temperature (±0.1 °C) was measured with a liquid-in-glass thermometer mounted inside the trap. Dissolved oxygen, oxygen saturation, pH, and conductivity were measured with a HACH HQ 40d electrode (oxygen and conductivity) and with a HANNA Combo electrode (pH and conductivity) inside the trap. The average conductivity from both electrodes was used. On 22 January 2012 (10:10-12:10) additional oxygen samples were collected at 5, 15, 35, 55, 75, and 95 m depths and titrated in the field within 2-4 hours following the WINKLER method (Winkler 1888).

In 2013, water samples were taken on 6 April starting at 1:30 pm with a 1.5 L Schindler-Patalas trap. Sampling was done at the deepest part of the lake reported by Thery et al (1995), where we measured a maximum depth of 110 m (14° 16.942’ S, 167° 32.298’ E, Secchi depth 1.3 m, Fig. 3). Temperature was recorded with a thermometer mounted inside the trap. Samples were taken from 0 m and at 100 m depth. Additionally, an integrated sample from 0-100 m depth at 10 m intervals (all depths equally included) was taken. All samples were filtered with pre-
combusted G/F filters (Whatman) using a 100 ml syringe tipped with a 50 mm filter holder (Sartorius). For each sample two 250 ml plastic bottles were rinsed with filtered water from the trap and filled to the top. One sample was acidified with 5 ml of 2M HCl to approximately pH 2, the other one was stored without preservation. Additionally for determination of total phosphorous, one unfiltered 125 ml sample was taken from 0 m and preserved with 2.5 ml of HCl. All samples were wrapped in aluminum foil, stored overnight in a river at approximately 20 °C, and from 7 April 2013 onward kept refrigerated at 2 - 4 °C until the analyses in the laboratory in Innsbruck on 16-19 April. On 7 April two 250 ml samples were taken from an inflowing hot spring (approximately 45 °C) at the northwestern end of the lake (14° 16.357' S, 167° 29.830' E) applying the same filter-, preservation, and storing method as described above. In the laboratory, conductivity was determined with a Tetracon 96 (WTW-LF 196) electrode. Ions (NO₃⁻, SO₄²⁻, Cl⁻, Na⁺, K⁺, Mg²⁺, Ca²⁺) were quantified through ion chromatography using a Dionex ICS 1000. Dissolved organic carbon (DOC) and dissolved nitrogen (DN) concentrations were analyzed from the acidified samples using a Total Organic Carbon Analyzer (Shimadzu TOC-Vc series) equipped with a Total Nitrogen Module (TNM-1). Both parameters were detected simultaneously after combustion and catalytic oxidation of the injected sample. Total phosphorous (Pₜₒᵗ), dissolved phosphorous (Pₜᵰₛᵣᵳ), and dissolved reactive silica (DRSi) were analyzed using the Molybdat - methods after Vogler (1966) and Smith and Milne (1981).

*Plankton organisms*

**Phytoplankton**

Phytoplankton samples were taken on 22 January 2012 at 0, 5, 15, 35, 55, 75, and 95 m depth. Approximately 1 L of water was filtered through a 10 µm mesh and preserved in Lugol’s solution. Additionally, algae were counted from 1.5 L of water (from 5, 15, 30 m) sampled on 21
January 2012, filtered through a 30 µm net and preserved in 4% formaldehyde. Additional qualitative 30 µm net samples collected in 2004, preserved and stored in 4% formaldehyde (Schabetsberger et al. 2009) were reanalyzed. Phytoplankton organisms were identified under an Olympus BX51 microscope and biomass was calculated according to the method of geometrical approximation (Rott 1981; Deisinger 1984) with eight reiterations on the Thoma blood-counting chamber. The identification was based on the standard phycological literature (e.g. Komárek and Fott 1983; Popovský and Pfiester 1990) and, when necessary, the synonymization was done according to relevant literature and Algaebase (Guiry and Guiry 2014).

Ciliates
As for phytoplankton samples (0, 5, 15, 35, 55, 75, and 95 m depth), approximately 1 L of water was filtered through a 10 µm mesh and equal sample volumes (50 ml) were preserved in Lugol’s solution for analysis of ciliates. Samples were stained with protargol after Skibbe (1994) and identified by using an Olympus BX51 microscope (brightfield contrast, magnifications up to 1,000 x) and 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 very well with protargol, but the different taxa could be well separated from each other.

Micrometazoa
On 21 January 2012 zooplankton samples were collected at 5, 15, 35, 55, 75, and 95 m depth (8:45-11:30). 1.5 L samples were filtered through a 30 µm plankton net and preserved with 2% formaldehyde. Around 3 h later the final concentration was raised to 4%. In the laboratory organisms were stained with Bengal Rose for at least 24 h. Copepods, and cladocerans were counted under a binocular (Reichert) at 25 x magnification, rotifers were counted with a Nikon Eclipse TS 100 inverted microscope using the sedimentation method after Utermöhl (1958).
**Macrophytes**

Aquatic plants were recorded along eight approximately 10 m wide transects (T1-T8) adjusted perpendicular to the shoreline and reaching from the shore to the vegetation limit in the depth (Fig. 3). The position of the start and ending points of the transects was determined by GPS (Garmin). According to Pall and Moser (2009) species spectrum and abundances were recorded separately for different depth zones by freediving, using a five level abundance scale reaching from 1 (very rare) to 5 (plentiful). The exact depth limit of the submersed vegetation in each transect was measured using a scaled line and weight. For species determination single plants were collected and preserved in alcohol (approximately 80% ethanol) or dried and stored in paper bags. Species were determined in the laboratory under a Motic BA 300 microscope (magnification 40 x - 1,000 x) and under a Reichert Type 300701 binocular (magnification 4 x - 45 x). The Relative Plant Mass for Lakes (RPM\textsubscript{L}) and the Mean Mass Index for Lakes (MMT\textsubscript{L}) were calculated according to Pall (1996).

<<Fig. 3 near here>>

**Eels**

In 2012 (January 17 – February 2) and 2013 (March 1 – April 4), eels were caught in Lake Letas and in Mbe Solomul river with handnets, by electrofishing, hooks, hook and line, and fyke nets in collaboration with local fishermen. Fish were measured and either released or sacrificed and given to the local population (Schabetsberger et al. 2013). The stomach contents of four *A. marmorata* and four *A. megastoma* from Lake Letas were counted in the field.
Results

*Physico-chemical depth profiles*

In 2012, temperature ranged from 27.6 °C at the surface to 23.8 °C in 95 m depth. A thermocline was observed between 10 (26.8 °C) and 20 m (24.7 °C). Beyond fifty meters depth, temperature remained constant (Fig. 4a). Temperature of the deep water layer (> 70 m) recorded in 2013 was slightly cooler (23.5 °C) than in 2012 (23.8 °C, Fig. 1a). Oxygen concentration measured with the electrode dropped from 7.10 mg L\(^{-1}\) at 10 m depth to 4.98 mg L\(^{-1}\) at 15 m, corresponding to 95.8 and 65.2 % saturation (Fig. 4b). Below the thermocline the oxygen level gradually decreased to 1.22 mg L\(^{-1}\) (15.7%) at 75 m depth. The deepest layer exhibited low oxygen levels ranging from 0.55 mg L\(^{-1}\) (7%) at 80 m to 0.28 mg L\(^{-1}\) (3.6%) at 95 m depth. The Winkler method showed the lowest oxygen level at 95 m with 0.1 mg L\(^{-1}\) remaining. Conductivity decreased from 614 µS cm\(^{-1}\) at the surface to 573 µS cm\(^{-1}\) at 30 m depth and was relatively constant below (Fig. 4c). The pH in the top 30 m decreased from 7.8 to 7.0. Below it slowly fell to 6.9 at 85 m depth and finally increased in the deepest layer to 7.1 (Fig. 4d).

<<Fig. 4 near here>>

Sulfate was the dominant anion in Lake Letas with values around 100 mg L\(^{-1}\) followed by chloride with 60 mg L\(^{-1}\) (Table 1). A strong depth gradient in nitrate from 8 (0 m) to 345 µg L\(^{-1}\) (100 m) was observed. Cations were relatively well mixed within the water column, dominated by magnesium and calcium. Total phosphorous at surface was 11.8 µg L\(^{-1}\) out of which approximately half was available as dissolved phosphorous. Concentrations of dissolved phosphorous increased 14-fold from surface to 100 m depth (6.2 to 87.9 µg L\(^{-1}\)). Maximum dissolved organic carbon (734 µg L\(^{-1}\)) and dissolved nitrogen (366 µg L\(^{-1}\)) were relatively low, whereas high values of dissolved reactive silica up to almost 17 mg L\(^{-1}\) were found. The water of
the hot spring was rich in ions with a relatively high content of nitrate, sulfate, chloride, potassium and calcium. It also supplied the lake with all four nutrients, with three- (P<sub>dis</sub>, DOC, DRSi) to tenfold (DN) concentrations compared to average lake values.

<<Table1 near here>>

Plankton organisms

Phytoplankton

In both qualitative and quantitative phytoplankton samples a total of 47 taxa were found (Table 2), some of which were tychoplanktonic from the bottom or plant substrates in the shallow lake area (e.g. Leptolyngbya foveolarum, Phormidium sp., Epithemia sp., Cymbella sp.). Euglenoid algae (free-living or in the stage of resting cysts), dinoflagellates, diatoms and cyanoprokaryotes were predominantly detected in these shore net samples. In the quantitative samples only typical planktonic algae appeared, with an obvious domination of green algae (chlorophytes and streptophytes). In the upper water layers the highest number of cells and the highest biomass belonged to the filamentous green alga Planctonema lauterbornii (0.244 mg L<sup>-1</sup> on average) followed by the biomass of the coccoid desmid Staurastrum depressiceps var. gracilis (0.186 mg L<sup>-1</sup>), while at depth of 95 m only few cells of the diatom Synedra sp. were seen. The species were commonly reported from tropical areas and are known to occur in a broad range of trophicity – from oligo- to eutrophic conditions. The species more typical for eutrophic standing waters were found in small amounts, sometimes in single coenobia or cells. The total biomass data in the epilimnion (0-15 m, average value of 1.06 mg L<sup>-1</sup>) showed the general mesotrophic character of the lake. In the deep hypolimnion 0.05 mg L<sup>-1</sup> of sedimenting algae were detected.

Ciliates

The ciliate assemblages in Lake Letas included several taxa that are commonly detected in lake plankton such as Halteria, Mesodinium, Coleps, Stentor and other prostomatids, haptorids and
scuticociliates (Table 3). In the sample that was pooled from 35 + 55 + 75 m, no ciliates were observed.

<<Table 3 near here>>

**Micrometazoa**

Nauplii and copepodids of *Thermocyclops crassus macrolasius* dominated the zooplankton community in the upper water layer, while the proportion of adults increased with depth (Fig. 5). The maximum abundance of the copepod with 138.0 Ind. L$^{-1}$ was detected in 5 m depth. Below 35 m few nauplii and female *T. crassus macrolasius* were found. *Diaphanosoma sarsi* reached highest abundance in the sample collected at 35 m (12.7 Ind. L$^{-1}$).

The rotifer community was poor. Only few individuals of *Anuraeopsis navicula, Hexarthra cf. fennica*, and undetermined Bdelloidea with a maximum total abundance of 7.4 Ind. L$^{-1}$ in 35 m were found.

<<Fig. 5 near here>>

**Macrophytes**

A dense macrophyte belt was discovered in seven of the eight transects investigated. Macrophytes were only absent at the north-western end of the lake (T6), where the outbreak of the volcano had extinguished most of the surrounding vegetation (Fig. 2a). The average vegetation limit was found in 4.8 m (standard deviation ±1.5 m) water depth, which corresponded to 75 m (±44 m) distance from the shore. In total, eight macrophyte species, including three species of Bryophyta (*Vesicularia* sp., *Ectropothecium* sp., *Hyophila* sp.) and one unidentified species of the family of Hymenophyllaceae, were recorded within three identified vegetation zones (Table 4). The most frequent species was *Ceratophyllum demersum*, which occurred in 18 out of 20 observed vegetated zones. However, the most abundant species was
Chara australis. Both species contributed 80 % to the overall plant mass of the macrophyte vegetation of Lake Letas (Fig. 6). Figure 7 shows the depth distribution of the single species as RPML values. In the “shallow zone” (0 to approximately 1 m depth) all macrophyte species found in the lake were present, however, the vegetation differed remarkably between transects probably due to differences in substrate and shoreline. On the flanks of the volcano (T4, T6 & T7), the substrate consisted mainly of sand and mud, while the rest of the lake was characterized by a rocky shoreline and a rocky and muddy substrate. Bryophyta were attached to rocks and overhanging trees, single Hymenophyllaceae were detected on the rocky shoreline of only one transect (T2). Single plants of Potamogeton pectinatus were found on submerged rocks. In the “middle zone” (1 – 3 m) the plant community was dominated either by Ceratophyllum demersum or Potamogeton nodosus. In the “deep zone” (3 m to vegetation limit) only Ceratophyllum demersum and Chara australis were present, where the latter formed a large macrophyte belt up to around 1 m height.

<<Fig. 6 near here>>
<<Fig. 7 near here>>

Eels

A total of 84 eels (40 A. marmorata, 36 A. megastoma, 8 A. obscura) were caught in Lake Letas (N=34) and Mbe Solomul river (N=50). Size ranges were 80 -142 cm in A. marmorata, 50 – 123 cm in A. megastoma, and 62 – 129 cm in A. obscura (Fig. 8). Only the former two species were found in the lake and hence their elvers surmount Siri Falls. The diet of four A. marmorata and four A. megastoma from Lake Letas (87 – 134 cm) contained predominantly various snails including Melanoides tuberculata, Fluviopupa sp., Gyraulus sp., and Glyptophysa cf. layardi (Gastropoda), as well as the backswimmer Anisops nasutus (Heteroptera), the dragonfly larvae of Macrodiplex cora, Orthetrum sabina/serapia, Anax guttatus, Rhyothemis sp., Agrionoptera sp.
and undetermined specimens of the Coenagrionidae (Odonata), one caddisfly species of the genus *Triplectides* (Trichoptera) and the freshwater shrimp *Macrobrachium lar* (Decapoda, Fig. 9).

Discussion

The maximum depth measured during the visits in 2012 and 2013 was 100 and 110 m respectively, corresponding closely to Baker’s (1929) records. The 119 m maximum depth reported by Thery et al. (1995) was not confirmed. This value was based on a single measurement and the maximum depth may have been overestimated due to a tilted position of the hydroacoustic transducer (e.g. from waves pounding at the dinghy in the middle of the lake). A more detailed hydroacoustic survey is desirable to construct a detailed bathymetric map and to potentially also estimate fish biomass.

Lake Letas was stratified and a thermocline existed between 10 and 15 m depth. The epilimnetic layer was characterized by temperatures above 26.8 °C, alkaline conditions (pH > 7.6), oxygen levels near saturation (>95%) and, in 2012, higher conductivity than in the hypolimnion. The surface layer probably undergoes frequent mixing due to wind action from the prevailing SE Wind along the 7 km long lake. However, relatively calm weather conditions preceded our sampling in 2012 and the mixed layer probably extends further down after intensive wind. In 2013 the thermocline was less pronounced and, in accordance to Baker (1929), found around 30 m depth. The large lake is surrounded by a low crater rim and obviously offers a large enough contact surface for wind action to ensure mixis all the way to the deepest strata. Below the thermocline temperature, pH, and conductivity gradually decreased down to a depth of 50 m. In the deeper hypolimnion comparatively weak gradients were observed, except
for oxygen, which decreased throughout the water column reaching almost anoxic conditions. However, even at 95 m depth traces of oxygen were confirmed with the electrode and the Winkler method, showing that this large lake is not meromictic throughout the year. In this respect it contrasts with several deep, meromictic volcanic crater lakes in Oceania whose sheltered position, smaller surface area, and inflow of salt water lead to anoxic conditions in the monimolimnion (Maciolek and Yamada 1981, Donachie et al. 1999, Sichrowsky et al. in press).

The high ion content at the lake surface in 2012 likely resulted from the inflow of ion-rich, warm volcanic spring water. In the North-East, an area called “Boiling Mud” had exhibited elevated ion concentrations (Schabetsberger et al. 2009). Conductivity in the hot spring was almost double the value in the epilimnion. Additionally, yellowish plumes of water seeping from the flanks of the volcano were observed (Fig. 2b). The strong thermal gradient probably prevented this ion-rich water from sinking immediately into the hypolimnion. On the other hand, the small increase of pH and conductivity near the sediment in 100 m depth could be an indication for solution of ions out of volcanic ashes. Conductivity in 2013 was probably reduced by dilution through previous rainfall. In 2012 and 2013, measurements were made before and after the main rainy season, respectively. Previous heavy precipitation could also be an explanation for the cooler water temperatures observed in 2013.

According to its sulfate and chloride concentration, which are, besides HCO₃⁻, the main products of the acidifying agents, and the pH, Lake Letas belongs to the group of quiescent volcanic lakes (Varekamp et al. 2000) or neutral HCO₃⁻ to SO₄²⁻-Cl⁻ waters (Marini et al. 2003). Superficial pH-values measured by Baker (1929; pH 8.5) and Schabetsberger et al. (2009; pH 8.9) were considerably higher than measurements in 2012 (pH 7.8). The increasing volcanic activity of Mount Garet after 2009 along with an elevated hydrothermal input likely acidified the lake.
With a total phosphorous concentration of 11.8 µg L⁻¹ the lake classified as mesotrophic (Table 1). Compared to the Secchi depth of only 1.3 m, which theoretically corresponds to approximately 50 µg L⁻¹ (Carlson 1977), this value appears low. Lower nitrate and dissolved phosphorous concentrations in surface layers and accumulation in the hypolimnion indicated nutrient uptake by phytoplankton and macrophytes. After total mixis, a fertilizing effect followed by enhanced algal growth seems likely. Dissolved nitrogen concentrations corresponded with nitrate, which was thus the predominant form of available nitrogen.

Hydrothermal activity supplied the lake with ion- and nutrient rich water. The hot spring showed elevated concentrations in sulfate, sodium, potassium and chloride and also in nutrients. Especially high silica concentrations provided a good nutrient supply for diatoms. The dissolved organic carbon likely originated from elution of volcanic ashes and burned vegetation and possibly through microbial production. However, it is unclear to what extent allochtonous DOC, which is often characterized by a slow decomposition rate, can contribute to the available carbon pool within the lake (Bade et al. 2007). Concerning phosphorous and nitrogen levels, the N:P ratio in the hot spring was 12, indicating a well-balanced ratio for primary production. At the lake surface, the ratio was lowered to 6.6, thus showing a trend for nitrogen limitation (Hellström 1996). This would give advantage to N-fixing cyanobacteria like *Anabaena*. However, since values are based on a single measurement and water samples were suboptimally stored until analyses, conclusions have to be treated with care. Nevertheless, with extensive hot inflows, Mt. Garet certainly has a fertilizing effect.

The detected phytoplankton species have a wide or even cosmopolitan distribution. Their resting stages are obviously readily distributed throughout Oceania by rain, wind, and animal vectors (Schabetsberger et al. 2009). The phytoplankton species assemblage was similar to this previous investigation, but the dominating species in the open water, *Planctonema lauterbornii*,
had not been recorded before. It may have appeared after the volcano became more active in 2009. This thermophilic species is known to form blooms under favorable conditions and to be in strong competition with the cyanoprokaryote *Planktolyngbya limnetica* (Nõges and Viirret 2001), which was found only as single filaments in the littoral samples. The total phytoplankton biomass of 1.06 mg L$^{-1}$ in the epilimnion confirmed the mesotrophic character of the lake. However, since phytoplankton samples were filtered, small algae were lost and values have to be interpreted with care.

The ciliates detected in Lake Letas included euplanktonic taxa commonly detected in temperate and tropical lakes (e.g., Beaver and Crisman 1989; Foissner et al. 1999, Table 3). However, characteristic prostomatids and oligotrichs such as *Balanion planctonicum*, *Urotricha* or *Rimostrombidium*, species that are known to efficiently graze on phytoplankton, were not found during this single sampling event possibly because they may be unable to produce resting cysts (e.g., Müller 1989, Sonntag et al. 2006). From the subclass Oligotrichia, only *Halteria* sp. was observed and the individuals appeared to possess algal symbionts. This so-called mixotrophic lifestyle is commonly found in ciliate plankton to sustain periods of low food supply or to gain sunscreen compounds (Esteban et al. 2010, Sommaruga and Sonntag 2009). *Coleps* and *Mesodinium* are very likely cosmopolitan ciliates that have recently also been recorded from Lakes Lalolalo and Lano on Uvea Island in Wallis and Futuna (Foissner et al. 1999, Sichrowsky et al. in press). Overall, the ciliate assemblages from three lakes on Uvea Island show more species-rich assemblages than in Lake Letas.

One copepod and one cladoceran species dominated the zooplankton. *Thermocyclops crassus macrolasius* likely has a distribution restricted to Austral-Asia and is not cosmopolitan as suggested by Mirabdullayev et al. (2003), but the species is pending for a revision. *Diaphanosoma sarsi* is a circumtropical species that is widely distributed on Pacific islands.
(Korovchinsky 2001). Both species reached highest abundances in the well-lit epilimnetic layer. Densities of planktonic Crustacea in the productive lake were twice as high as encountered in freshwater crater lakes on Wallis and Futuna (Sichrowsky et al. in press). In contrast, rotifers were with a maximum abundance of 7 Ind. L\(^{-1}\) almost nonexistent in Lake Letas.

Lake Letas was characterized by dense macrophyte vegetation. Lower abundances could only be found along the flanks of the volcano Mount Garet, reflecting either the aftermaths of the eruption in 2009 or the recent influence of turbid and ion-rich seepage water. According to information by locals macrophytes were present before the outbreak in the now unvegetated north-western area (Chief Paul Lazarus, Gaua, personal communication). The average depth limit of the macrophyte vegetation was 4.8 m which theoretically corresponds to a Secchi depth of 2.7 m (Chambers and Kalff 1985, Middleboe and Markager 1997). Therefore it is likely that the Secchi depth in Lake Letas usually is higher than that measured during the investigation (1.3 m). Furthermore, a higher Secchi depth would fit better to the mesotrophic status of the lake.

The three vegetation zones found can be regarded as typical for meso- to eutrophic lakes. In the “shallow zone” narrow-leaved pondweeds (\textit{Potamogeton pectinatus}) were dominant, in the “middle zone” broad-leaved pondweeds (\textit{Potamogeton nodosus}) built a “pondweed-belt”, and in the “deep zone” charophytes (\textit{Chara australis}) represented the dominant vegetation. However, from the species spectrum found, eutrophic conditions can be deduced. Most of the species, namely \textit{Ceratophyllum demersum}, \textit{Potamogeton nodosus} and \textit{P. pectinatus} are highly eutraphentic (Casper and Krausch 1980, 1981). Charophytes, in contrary, are usually restricted to oligotrophic or mesotrophic conditions (Forsberg 1965, Krause 1997). Accordingly e.g. Green (1975) found \textit{Chara australis} in Lake Ototoa, an oligotrophic sand-dune lake in New Zealand. The main reason for the dominant occurrence of \textit{Chara australis} in Lake Letas might be the high
potential of this species to recover following any destruction of its plant stands (Wood and Mason 1977).

Most of the macrophyte species found are cosmopolitan (**Ceratophyllum demersum**, **Potamogeton nodosus** and **P. pectinatus**). Only **Chara australis** is restricted to the southern hemisphere (Wood and Mason 1977).

Lake Letas and its effluent river provide a unique habitat for freshwater eels. Assuming that around 25 °C eels can tolerate oxygen concentrations below 3 mg L⁻¹ (Molnár 1993; Cruz-Neto and Steffensen 1997), they can potentially populate the lake down to below 50 m depths. This includes the vegetated slope area with high abundance of benthic food organisms. Stomach contents did not indicate cannibalism and also has not been observed by local fishermen (Chief Victor Wotias, Gaua, personal communication). As no other fish are able to surmount Siri falls, the eels are free to exploit the rich food resources in Lake Letas. In the lower stretches of Mbe Solomul river the largest *A. obscura* hitherto reported in literature was caught (129 cm). Our data show that the lake and its effluent river are a habitat of primary importance to Pacific eels. With declining stocks observed in temperate eel species (Aoyama 2009, Tsukamoto 2009) pressure on tropical eels might increase. Hence, efforts should be made to protect Lake Letas and his effluent river from possible threats.

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Figure 1. (a) Northwestern and (b) southern end of Lake Letas with seepage of water from the flanks of Mount Garet.
Figure 2. Map of Gaua Island and Lake Letas.
Figure 3. Bathymetric map of Lake Letas redrawn after Thery et al. (1995). T1 – T8 indicate the locations of transects for macrophyte recordings. Maximum depth of 110 m was measured using line and weight.
Figure 4. Depth profiles of (a) temperature, (b) oxygen, (c) conductivity, and (d) pH in Lake Letas on 19 January 2012 (before the main rainy season). Temperature in 2013 was measured on 6 April (at the end of the main rainy season).

Figure 5. Crustacean zooplankton of Lake Letas on 21 January 2012.
Figure 6. Relative Plant Mass ($RPM_L$) of the single species / taxonomic groups in Lake Letas.
Figure 7. Depth distribution of the single species / taxonomic groups in Lake Letas (RMP$_L$).
Figure 8. Size ranges of *A. marmorata*, *A. megastoma*, and *A. obscura* caught in Lake Letas and Mbe Solomul river.
Figure 9. Diet of four *A. marmorata* and four *A. megastoma* caught in Lake Letas (87 -134 cm).
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