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Authors: Schabetsberger, Robert, Drozdowski, Gabriele, Rott, Eugen,

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Losing the Bounty? Investigating Species Richness in Isolated Freshwater Ecosystems of Oceania¹

Robert Schabetsberger,^{2,3} Gabriele Drozdowski,³ Eugen Rott,⁴ Rupert Lenzenweger,⁵ Christian D. Jersabek,³ Frank Fiers,⁶ Walter Traunspurger,⁷ Nicola Reiff,⁸ Fabio Stoch,⁹ Alexey A. Kotov,¹⁰ Koen Martens,⁶ Heinrich Schatz,¹¹ and Roland Kaiser³

Abstract: The South Pacific freshwater ecosystems have never been investigated systematically. Although their ecological value has long been recognized and recommended for protection, little action has been taken so far. Here, we present results of 39 lentic water bodies on 18 islands belonging to seven countries. Temperature, conductivity, and pH were measured and samples of aquatic organisms were collected. Freshwater algae, nematodes, rotifers, ostracods, copepods, cladocerans, and aquatic oribatid mites were identified to genus or species level. Sixty-six percent of all taxa recorded have a cosmopolitan distribution, 14% are circumtropical/tropicopolitan species, and for 20% a restricted distribution predominantly in Australasia has previously been reported. Eleven new copepod and three new ostracod taxa were discovered. Out of 39 water bodies we found at least 17 stocked with nonindigenous fish species. Salinization and uncontrolled introduction of alien fish species may lead to reduced species richness in these remote freshwater ecosystems. The highest species richness was recorded in old, shallow, fish-free softwater lakes at high altitude.

THE SOUTH PACIFIC islands harbor some of the most isolated freshwater lakes of the world. Most of them fill volcanic craters that formed thousands of kilometers away from

Pacific Science (2009), vol. 63, no. 2:153–179 © 2009 by University of Hawaiʻi Press All rights reserved the next continent. These small islands of freshwater habitat surrounded by a vast saline water mass are ideal targets for ecological and biogeographic research. Although their ecological value has long been recognized (Dahl 1980), up to now only one lake is protected as a national park (Lake Lanotoʻo, Samoa); however, even this lake remains so ill-explored that its depth was unknown before our visit.

A limited number of freshwater plankton and benthos organisms colonized these lakes through long-distance dispersal probably via resistant propagules carried by wind, rain, animal vectors, or humans (for recent reviews see Bilton et al. 2001, Bohonak and Jenkins 2003, Havel and Shurin 2004, Panov et al. 2004, Green and Figuerola 2005, Vanschoenwinkel et al. 2008). The relative importance of the different vectors is still unknown, and as Bohonak and Jenkins (2003:785) stated, "Despite its noble pedigree, our knowledge base regarding passive dispersal in freshwater invertebrates has progressed little since Darwin's time."

In higher plants and animals the low number of colonizers radiated into extensive

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² Corresponding author.

³ Division of Organismal Biology, University of Salzburg, Hellbrunnerstrasse 34, A-5020 Salzburg, Austria (e-mail: Robert.Schabetsberger@sbg.ac.at).

⁴ Institute of Botany, University of Innsbruck, Sternwartestrasse 15, 6020 Innsbruck, Austria.

⁵ Schlossberg 16, 4910 Ried im Innkreis, Austria.

⁶ Royal Belgian Institute of Natural Sciences, Vautierstraat 29, 1000 Brussels, Belgium.

⁷ Animal Ecology, University of Bielefeld, Morgenbreede 45, 33615 Bielefeld, Germany.

⁸ The Bavarian State Collection of Zoology, Münchhausenstrasse 21, 81247 Munich, Germany.

⁹ Via dello Sboccatore 3/27, 00069 Trevignano romano (Roma), Italy.

¹⁰ A. N. Severtsov Institute of Ecology and Evolution, Leninsky prospect, 33, 119071 Moscow, Russia.

¹¹ Institute of Ecology, University of Innsbruck, Technikerstrasse 25, 6020 Innsbruck, Austria.

insular species complexes. Today the Pacific islands present one of the highest levels of endemism in the world. With decreasing distance to the Asian and Australian continent, the total number of animal and plant species found on each island increases, and the number of endemic species decreases (Loope 1998).

Whether the same evolutionary forces are shaping freshwater protist, algal, and micrometazoan communities is a matter of debate. Fenchel and Finlay (2004) argued that dispersal is rarely (if ever) restricted by geographical barriers and that propagules (diapausing resting eggs or cysts) up to 1 mm might disperse globally. To the contrary, Foissner (2004) and Kristiansen (2005) argued that there is indisputable evidence of endemism and restricted geographical distribution in at least some protist species. Similar opposing views exist for several groups of freshwater microalgae (mainly diatoms, blue-green algae/cyanobacteria, and desmids [Kristiansen 1996]) and micrometazoa (Frey 1982, Dumont 1983, Dumont and Segers 1996, Reid 1997).

Theory predicts that we should find higher species richness in old, deep, productive lakes on large islands closer to a continental land mass (Green 1992). According to the equilibrium model of McArthur and Wilson (1967) immigration rates were most likely positively related to dispersal vectors such as wind or birds as well as target island/lake size and negatively related to "source to target" distance (see also Whittaker 1998). Current-day community composition in isolated South Pacific freshwater bears the imprint of local processes (e.g., habitat suitability, competition, predation, disturbance) that limit the diversity in individual communities, whereas regional processes (e.g., immigration, speciation) should enrich local communities (He et al. 2005. Hessen et al. 2006).

Detailed surveys of algae and micrometazoa are available for the Hawaiian Archipelago (e.g., Jersabek 2003, Sherwood 2004), but comparatively little limnological research has been conducted on South Pacific islands, due to the remoteness and low accessibility of many freshwater ecosystems. Descriptive

studies on lake morphology and physicochemical variables together with short paragraphs on flora and fauna are available only for Tagimaucia crater lake on Taveuni Island, Fiji (Southern et al. 1986), and the Vai Lahi crater lake on Niuafo'ou Island, Tonga (Maciolek and Yamada 1981). Species lists of nematodes, rotifers, and microcrustaceans are available for Easter Island (Segers and Dumont 1993, Dumont and Martens 1996) and the Galápagos Islands (DeSmet 1989a,b, Segers 1990, Eyualem and Coomans 1995); older data refer to Melanesia and Micronesia (Lindberg 1954). Meisch et al. (2007) presented a list of ostracods described from Oceania. Chappuis (1955), Yeatman (1983), and Dussart (1984) reported harpacticoids from Fiji, Western Samoa, Tonga, and New Caledonia. Taxonomic descriptions of New Caledonian copepods were provided by Dussart (1984, 1986) and Defave (2001) and for cladocerans by Timms (1985). Korovchinsky (2001) reviewed the cladoceran family Sididae and described the new species Diaphanosoma samoaensis from Lake Lanoto'o on Samoa. Older records of different crustacean species are available from Sars (1904), Stingelin (1905), Jenkin (1929), and Lowndes (1928, 1931).

The species richness in these lakes may be reduced by a number of different threats. Alien fish species have been introduced into the majority of suitable freshwater habitats and may alter plankton and benthos communities (Schindler and Parker 2002). In addition, societal demands have contributed to environmental degradation (i.e., forest clearance and logging [also by pre-European settlers, as described by Rolett and Diamond 2004], commercial development and urban sprawl [Schuster et al. 1996]). Finally, the Pacific island nations will be among the first to experience adverse impacts of climate change. Rising sea levels will eventually lead to coastal erosion and saline intrusions.

The aim of this study was to measure abiotic variables and collect samples in 39 South Pacific freshwater ecosystems listed in Scott's (1993) Directory of Wetlands in Oceania. Species lists for algae, nematodes, rotifers, copepods, cladocerans, ostracods, and mites

(Oribatida) are presented. We also discuss our results in respect to potential threats to freshwater ecosystems and provide recommendations for future research.

MATERIALS AND METHODS

Sampling Sites

The majority of water bodies were volcanic crater lakes (Nos. 12, 13, 15-29, 31-34, 36, 37 [Plate 1, Table 1]). Lake Vaihiria (1) on Tahiti was originally formed by a rock slide. Together with Lake Bleu (2), the two water bodies are artificially dammed for hydropower. On the Cook Islands the freshwater runoff from the basaltic volcanic cone is collected at the inner cliff of an old fringingreef surface that has been exposed through tectonic uplift (Makatea [Ellison 1994, Parkes 1997] [3, 4, 6, 10]). The underground drainage in the Makatea is occasionally open to the surface at partly collapsed karst caves (often referred to as "Vai" for "freshwater" [5, 7, 8, 9, 11]). Similar openings in the karst water system are found in Vanuatu (30, 35). Lake Isiwi on Tanna was originally dammed by the active volcano Mount Yasur but drained in 2000. Only a few puddles remained near the outflowing river (39). In a few cases the formation of the lake basin was not obvious (14, 33, 38).

Some craters in Fiji were probably formed more than 2 million years ago (Nunn 1998 and pers. comm.), but most of them are younger. All lakes that depend on the water table of the entire island must have been dry during the last glacial maximum when the sea level in the tropical Pacific was 120 m below current level. Most of them started filling again in the Early (10,000-6,000 B.P.) or the Middle Holocene (6,000-3,000 B.P.) when the sea level was 1.5–2.0 m above its current level (Nunn 1999 and pers. comm.). The Manaro lakes on Ambae, Vanuatu, are only 420 yr old. Fourteen years ago, Lake Manaro Vui (29) underwent strong heating due to volcanic activity, and water levels fluctuated ~10 m within 3 days (Robin and Monzier 1995). In 2005, a new crater started to rise within the lake.

Sampling and Species Identification

Water bodies classified as freshwater ecosystems were chosen from the compilation of wetlands in Oceania (Scott 1993). Additional inland aquatic ecosystems were located on various geographic maps and aerial photographs. Finally, R.S. and G.D. sampled a total of 39 different water bodies on 18 different islands (Table 1). Conductivity, pH, and temperature were measured at the water surface with a portable device (Hanna Instruments). The presence of fish was assessed by observation from shore or by snorkeling. A lake containing solely eels was not classified as a "fish-lake" because eels are predators and do not feed on detritus or zooplankton. In this respect, all "fish-lakes" likely were stocked, although time constraints, difficult accessibility, or turbid water prevented us from determining species in three cases and from assuring presence or absence of fish in seven cases.

Plankton samples were collected with a 30 μm plankton net (21 cm diameter). Shallow water bodies (<1 m) were sampled either by scooping up water with a beaker or by throwing out and retrieving the net from shore. In larger lakes we swam with the net and dived down to a depth of approximately 5 m. When macrophytes were present the net was dragged through them; however strictly benthic microhabitats (e.g., different sediments) were not targeted specifically. Twenty-five ml of each sample were preserved in 4% formaldehyde. In the laboratory species were isolated under a stereomicroscope, prepared on slides, and identified to genus or species level: algae (excluding desmids and most diatoms) by E.R.; desmids by R.L.; nematodes by N.R. and W.T.; rotifers by R.S. and C.D.J.; cyclopoid copepods by F.S.; harpacticoid copepods by F.F.; cladocerans by A.A.K.; ostracods by K.M.; oribatids by H.S.

Information is provided where the different taxa so far have been reported to occur. We chose the terms circumtropical, tropicopolitan, cosmopolitan, and restricted distribution. In the literature, the different terms are used inconsistently to describe distributions, and the geographic or climatic definitions

TABLE 1 Lentic Freshwater Ecosystems Sampled on South Pacific Islands

Sub- mersed Vege- tation b	1 1	I	+	I	ı	I	ı	I	I	I	+ +	-	I	I	ı	+	Ι	I	I	1 1	ı	+
Active Volca- nism b	1 1	I	I	I	1	I	I	I	I	I	1 1	I	I	ı	I	I	Ι	Ι	I		I	I
Fish"	T?, G, S G	T, G	Ë	۲.	T,+	+	I	M	T, M	+	1 1	Т	F	· [L	I	<u>۲</u> .		9	1 1	1	I
Cond. (µS cm ⁻¹)	86 97	1,693	52	2,560	>4,000	1,852	724	1,038	>4,000	2,486	11 4	4	29	i &	1,583	30	28	35	n v	υ 4	26	10
$^{ m hd}$	9.75	7.37	6.71	7.76	8.28	8.18	7.84	7.88	8.54	7.77	6.55	7.40	7.47	8.85	8.79	4.14	8.85	7.13	2.72	5.99	6.50	5.07
Femp.	23.4 25.0	27.6	25.7	23.6	26.1	23.5	23.6	22.6	27.5	23.6	21.7	27.5	31.0	30.6	30.2	33.9	34.7	35.7	8.72	27.4	24.8	23.6
Area Depth Temp (ha) (m) (°C)	22 \$\$	\Diamond	\Diamond	\$	2	$\stackrel{\diamond}{\sim}$	0.2	<10	7	\$	1> 12 5	, ∞			20	I	\Diamond	∵ ∵	15.2	1.5-5	2.7	1.5–3
Area (ha)	16–22	150	I	0.008	100	0.003	<0.001	0.001	E	0.001	0.6	1.5	87	~	18	0.001	1.5	S	00	0.0	0.8	4
Alt. (m)	473 380	~	20	~	I	5	~	20	20	~	800	230	"	'n	7	10	35	9 (79/	670 670	885	964
Latitude	17°40′57.28″S 17°41′25.19″S	21°57′04.52″S	21°54′31.47″S	19°51′46.43″S	19°52′08.94″S	19°51′53.60″S	19°53′03.99″S	20°00′42.24″S	20°00′34.44″S	19°59′07.40″S	16°49′52.56″S 16°49′07.17″S	16°24′55.82″S	13°17'40.39"S	13°19′13.28″S	13°18′01.72″S	13°18′56.57″S	13°18′57.03″S	13°17′43.64″S	13°54′39.29″S	13°54′28.69″S	13°56′15.76″S	13°57′13.70″S
Longitude	149°24′58.78″W 149°25′05.62″W	157°55′41.67″W	157°55′31.15″W	157°42′51.56″W	157°41′19.62″W	157°40′57.47″W 19°51′53.60″S	157°41′36.89″W 19°53′03.99″S	158°07′21.35″W	158°07′22.48″W	158°05′40.73″W	179°58′34.54″W 179°56′07.30″W	179°39′39.33″E	176°14′24 48″W	176°12′52.48″W	176°14′06.41″W	176°13'01.77"W	176°12′36.23″W	176°11′18.53″W	1/1°49′32.63″W 171°50′48 00″W	171°50′25.92″W	171°45′14.57″W	171°40′56.36″W
Country	France France	Cook Islands	Cook	Cook Cook	Cook	Islands Cook	Islands Cook	Islands Cook	Islands Cook	Islands Cook	Islands Fiji Fiji	Eji	France	France	France	France	France	France	Samoa	Samoa	Samoa	Samoa
Island	Tahiti Tahiti	Mangaia	Mangaia	Mitiaro	Mitiaro	Mitiaro	Mitiaro	Atiu	Atiu	Atiu	Taveuni Tevenni	Vanua	Levu Wallis	Wallis	Wallis	Wallis	Wallis	Wallis	Upolu	Cpolu	Upolu	Upolu
Name	Vaihiria Bleu	Tiriara	Kauravai	Vai Marere	Rotonui	Vai Nauri	Te Pito o Kare	Vai Rimarau	Tiroto	Vai Momoiri	Aselemo* Tagimancia	Navesiwaka	Lano	Lanutavake	Lalolalo	Lanutuli*	Lanumaha	Kikila I	Lanoto o	Lanoanea*	LePue	Fit:
Date	17.09.2004 17.09.2004	21.09.2004	22.09.2004	24.09.2004	25.09.2004	25.09.2004	25.09.2004	28.09.2004	28.09.2004	29.09.2004	05.10.2004	15.10.2004	01 11 2004	01.11.2004	02.11.2004	02.11.2004	02.11.2004	03.11.2004	15.11.2004	15.11.2004	20.11.2004	23.11.2004
Water Body No.	7	3	4	5	9	7	∞	6	10	11	12	4.	15	16	17	18	19	50	17	23	24	25

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1 1 + -	⊦ I	+	+		ı	ı	+	Ι	+	+	I	+
350 M 598 T, M 6 ->	1,070 +	555 5				54 +5	1,946 -	2,656 +	>4,000 T		>4,000 +	153 –
	7.13	8.90	6.46		6.65	9.03	8.04	6.91	8.62			8.00
	26.5	26.7	36.6		27.7	30.3	30.6	27.0	29.0	30.2	32.5	32.6
1.3	10	360	360		I	<10	252	1.5	107		$\stackrel{\sim}{\sim}$	0.3
10 6 170	0.7	1,900	1,900		0.7	30	815	< 0.001	1,400	20	6.4	< 0.001
1,397	5	418	418		280	119	20	7	2	0	0	09
15°17′08.35″S 15°17′02.89″S 15°23′09.57″S	15°18′47.85″S	14°16′44.03″S	14°15′27.58″S		16°45′40.29″S	17°43′59.55″S	19°44′33.83″S	15°57′22.54″S	15°36′05.84″S	15°36′05.00″S	15°32′16.75″S	19°31′22.29″S
	167°10′11.31″E	167°32′29.41″E			168°13′06.20″E 1	168°24′52.85″E	175°03′48.71″W	173°47′52.28″W	175°37'07.97"W 15°36'05.84"S	175°37′03.15″W	167°11′57.78″E	169°26′05.98″E
	Vanuatu	Vanuatu	Vanuatu			Vanuatu		Tonga	u Tonga	Tonga	Vanuatu	Vanuatu
	te Espiritu Santo	Gana	Gana	lai	Epi	Efate	Tofua	Niuato-	Niuafo'ou	Niuafo'ou	Aori	Tanna
Wai Lembutaga Wai Memea Manaro Kesa (Lakua)	Shark Bay Blue Hole	Letas	Letas	hydrothermal vent	Imao*	Duck	Tofua	Niuatoua	Spring Vai Lahi	Vai Si'i	Aori	Isiwi*
04.12.2004 02.12.2004 05.12.2004	11.12.2004	15.12.2004	16.12.2004		22.12.2004	28.12.2004	11.01.2005	19.01.2005	20.01.2005	20.01.2005	10.12.2004	29.12.2004
26 27 28 28	30	31	31		32	33	34	35	36	37	38	39

Note: Approximate values are in italics.
*, Potentially temporary.
" T, tilapias (Orochromis spp., Sarutherodon spp.); G, guppies (Poecilia reticulatu); S, swordtails (Xipbophorus bellerii); M, mosquitofish (Gambusia affinis); Go, goldfish (Carassius auratus); +, fish present, species unknown (not counting Anguilla spp.); +?, fish presence likely; -, fish presence unlikely.

b +, present; -, absent.

are seldom provided (e.g., pan-, cosmo-, circumtropical, tropicopolitan). Our definitions follow.

Circumtropical: Species that have primarily been reported from tropical environments between the Tropics of Cancer (23°27′ N) and Capricorn (23°27′ S).

Tropicopolitan: Organisms that are frequently found throughout the tropical and subtropical zones (up to approx. 34° N and S) but that do occur at higher latitudes, if local temperature regimes permit.

Cosmopolitan: Species that are found worldwide. The occurrence in polar regions or high-altitude environments is not confirmed in every case.

Restricted distribution: Species that so far have been found only in a restricted area (e.g., Australasia: the islands of the southern Pacific Ocean, including Australia, New Zealand, and New Guinea).

Statistical Analysis

The exploratory power of different environmental variables to predict overall species richness was tested using Generalized Linear Models (GLM [McCullagh and Nelder 1989]): archipelago (seven levels: Tahiti, two sites; Cook Islands, nine; Fiji, three; Samoa, five; Wallis, six; Tonga, four; Vanuatu, nine), fish (two levels: present, absent), submersed vegetation (two levels), active volcanism near water body (two levels), and eight continuous variables (log conductivity, pH, temperature, log surface area, log maximum depth, log [altitude + 1], geographical longitude, and latitude). Conductivity, altitude, maximum depth, and surface area were log transformed due to skewed data. Acid Lake Manaro Vui contained no living organisms and was omitted from the analysis.

Community composition was analysed with Nonlinear MultiDimensional Scaling (NMDS [Kruskal 1964]) using presence-absence data of all determined taxa and the environmental variables. The Bray-Curtis index was calculated because it performs well in detecting underlying ecological gradients. The analysis was done with the R package Vegan (Oksanen et al. 2007) following Minchin (1987).

In ordination, fitted vectors (biplot arrows) have become the method of choice for testing environmental variables. However, traditional linear fits onto ordination diagram models may yield poor fits, due to curvature and distortion in ordination space. Given these restrictions, we additionally applied *Thin-Plate Splines* (TPS) estimated with *General Additive Models* (GAM [Wood 2003]). TPS interpolate a smooth surface passing through the values of environmental variables. To assess significance levels of fitted vectors and factors, 1,000 permutations were run.

Because communities within an archipelago were similar, they were chosen as permutable units for a third approach in statistical analysis. NPMANOVA (NonParametric Multivariate ANalysis Of VAriance) is a method in which simultaneous responses of several, potentially nonindependent variables (usually species in an assemblage) are compared in a one-factor or multifactorial ANOVA setting (Anderson 2001, McArdle and Anderson 2001). P values were obtained by 4,999 permutations.

RESULTS

Sampling Sites

A distance of approx. 4,500 km separates the eastern- and westernmost sampling sites, in Tahiti and Vanuatu, respectively (Plate 1, first panel). The sampled water bodies covered a broad range in altitude (0-1,397 m above sea level [a.s.l.]), surface area (>0.001-1,900 ha), depth (10 cm-360 m), temperature (19.5°C-36.6°C), pH (1.56–9.75), and conductivity $(3->4,000 \mu S cm^{-1} [Figure 1])$. Ion content showed a bimodal distribution with the majority of sampling sites being either softwater or slightly saline environments. Crater lakes near sea level ranged from pure freshwater to almost oligohaline conditions (Table 1). Increased ion content has also been observed in water bodies with no adjacent volcanic activity and most likely resulted from an underground connection to the sea. Lake Manaro Vui was acidic (pH 1.56) due to volcanic activity and contained no living organisms.









PLATE 1. Sampling sites in Oceania (first panel) and photographs of South Pacific freshwater ecosystems taken during the survey in 2004/2005 (subsequent panels).









PLATE 1 (Continued).









PLATE 1 (Continued).













PLATE 1 (Continued).













PLATE 1 (Continued).













PLATE 1 (Continued).













PLATE 1 (Continued).

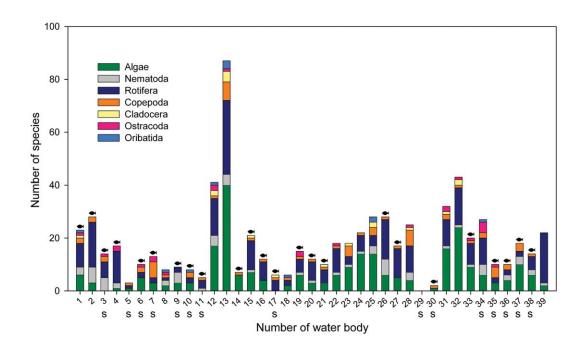


PLATE 2. Cumulative number of species of the major groups of organisms in the 39 different water bodies. Stocked ecosystems are marked by a fish symbol above the bar. Elevated conductivity (> $1000~\mu S~cm^{-1}$) is indicated by an "s" below the x-axis.

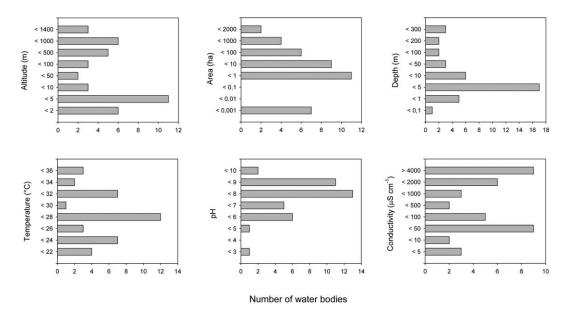


FIGURE 1. Number of water bodies in relation to altitude, area, depth, temperature, pH, and conductivity.

Fish Species

Of the 39 sampled water bodies, at least 17 contained large numbers of one or more non-indigenous fish species (Table 1). We encountered tilapias (*Oreochromis* spp., *Tilapia* spp., *Sarotherodon* spp.) mosquitofish (*Poecilia reticulata*), guppies (*Gambusia affinis*), swordtails (*Xiphophorus hellerii*), and goldfish (*Carassius auratus*). Native freshwater eels were observed in Lake Rotonui (*Anguilla obscura*) and Lake Letas (*A. marmorata* or *A. megastoma*), but different species of eels are reported by locals to occur in all larger crater lakes. Endemic fish (e.g., Gobiidae or Eleotridae) were not observed. They are amphidromous and probably restricted to lotic ecosytems.

Species Richness and Community Composition

A total of 138 algal, 36 nematode, 98 rotifer, 32 copepod, nine cladoceran, nine ostracod, and four oribatid taxa were identified (Appendix). The highest cumulative species numbers were found in dormant and shallow craters filled with vegetation such as Lakes Aselemo and Tagimaucia (Fiji), Fiti (Samoa), and Imao (Vanuatu) (Plate 2).

ANALYSES: GLM: STATISTICAL testing the exploratory power of all variables on species richness, a simplified model was built containing archipelago (P < .001), log conductivity (P < .001), submersed vegetation (P < .001), and fish (P = .026) in linear combination (Table 2). No significant interactions were observed. Model results are presented in the form of a deviance table, which is analogous to an ANOVA table, except that the variance component reported is the deviance rather than the sums of squares (see McCullagh and Neldar [1989] for a full discussion of deviance and Generalized Linear Models). Altitude negatively correlated conductivity (Pearson's R = -0.79, P < .001). The deviance explained by both variables was nearly the same, so we decided to use conductivity in the model to facilitate ecological interpretation.

NMDS (Table 3): A significant spatial effect was detected and communities were more similar within an archipelago (P < .001). A weak but significant effect was also found for active volcanism (P = .026). Log conductivity (P < .001) and log altitude (P < .001) were the most important factors explaining community composition. In addition, geographi-

Variable	df	Deviance	Residual df	Residual Deviance	P	Significance ^a
Null			37	345.98		
Archipelago	6	156.15	31	189.73	<.001	***
Log conductivity	1	27.50	30	162.23	<.001	***
Submersed vegetation	1	31.62	29	130.61	<.001	***
Fish	1	9.09	28	121.51	.026	*

TABLE 2
Analysis of Deviance Table (Generalized Linear Model)

Note: The response variable is species richness. The error distribution is Poisson with log link. a^* , P < .05; ***, P < .001.

TABLE 3

Linear Fit of Environmental Variables on Community Composition (Two Dimensions of Nonlinear Multidimensional Scaling)

Variable	R^2	P	Significance ^a
Archipelago	0.497	<.001	***
Active volcanism	0.092	.026	*
Fish	0.042	.211	
Submersed vegetation	0.015	.592	
Log conductivity	0.536	<.001	***
Log altitude	0.528	<.001	***
Latitude	0.162	.045	*
Log surface area	0.134	.078	
Longitude	0.069	.296	
Surface temperature	0.056	.381	
Log maximum depth	0.056	.368	
рH	0.051	.390	

^{a*}, P < .05; ***, P < .001.

cal latitude (P = .045) explained a significant amount of species dispersion.

GAM (Table 4): Thin-plate splines added surface temperature (P = .010) and longitude (P = .027) as weakly significant variables.

NPMANOVA (Table 5): Significant effects of pH (P = .028) and submersed vegetation (P = .020) emerged.

Distribution

Sixty-six percent of all taxa recorded have a cosmopolitan distribution, 14% are circumtropical/tropicopolitan species, and for 20% a restricted distribution predominantly in Australasia has previously been reported. Crustaceans comprised a lower number of cosmopolitan taxa compared with algae, nematodes, rotifers, and oribatid mites (Figure 2).

DISCUSSION

Distribution and Taxonomic Status

ALGAE: Although a large proportion of the mostly planktonic algae (excluding desmids) are supposed to have a cosmopolitan (60%) distribution, 38% can be grouped into circumtropical (18%) and tropicopolitan (20%) taxa, respectively (Figure 2). The proportion of circumtropical/tropicopolitan taxa is high compared with 19% in a recent Southeast Asian study (Rott et al. 2008). The majority of desmids were cosmopolitan species (Appendix). Out of 54 taxa, 14 are assigned to the Indo-Malaysian North Australian phycogeographic region (sensu Coesel [1996] and Vyverman [1996]). Staurastrum aureolatum was recorded from Australia, New Zealand, and South Africa (Croasdale et al. 1994).

TABLE 4
Fit of Thin-Plate Splines of Continuous Environmental Variables to Community Composition (Fitted by a
Generalized Additive Model onto Two Dimensions of Nonlinear Multidimensional Scaling)

Variable	Deviance	F	P	Significance ^a
Latitude	0.681	7.013	<.001	***
Log altitude	0.672	7.695	<.001	***
Log conductivity	0.640	6.846	<.001	***
Surface temperature	0.478	3.084	.010	*
Longitude	0.384	2.508	.027	*
pH	0.331	2.179	.051	
Log surface area	0.134	2.714	.080	
Log maximum depth	0.056	1.039	.364	

^a *P < .05; ***, P < .001.

TABLE 5

Effects of Environmental Variables on Community Composition (NPMANOVA on Bray-Curtis Distances)

Variables	df	SS	F	R^2	P	Significance ^a
Archipelago	6	4.731	2.230	0.301	.375	
Log conductivity	1	1.343	3.369	0.086	.006	**
Log altitude	1	1.163	2.883	0.074	.008	**
Latitude	1	1.154	2.856	0.074	.423	
pН	1	0.814	1.971	0.052	.028	*
Longitude	1	0.798	1.928	0.051	.044	*
Volcanic activity	1	0.686	1.646	0.044	.337	
Fish	1	0.656	1.570	0.042	.074	
Temperature	1	0.595	1.420	0.038	.271	
Submersed vegetation	1	0.582	1.388	0.037	.020	*
Log maximum depth	1	0.558	1.326	0.036	.285	
Log surface area	1	0.555	1.321	0.035	.371	
Total	37	15.693				

Note: Permutations are stratified by archipelago.

NEMATODES: Except for four species, the nematodes are probably all cosmopolitan, but information on distribution is scarce. *Dichromadora* cf. *tobaensis* has only been reported from Sumatra (Andrássy 1984), *Mesodorylaimus* cf. *guarani* from Paraguay and Costa Rica (Ahmad and Shaheen 2004), *Mesodorylaimus* cf. *meyli* from Eurasia (Vinciguerra 2006), and *Neoactinolaimus* cf. *duplicidentatus* from Eurasia and Africa (Vinciguerra 2006).

ROTIFERS: More than 90% of all rotifers were widely distributed species. The remainder were predominantly species that were described in the recent past and for which biogeographic information is scarce (e.g.,

after its discovery in a high-altitude lake in southern India *Polyarthra indica* [Segers and Babu 1999] has now been found in Africa [Schabetsberger et al. 2004] and throughout the Pacific islands, suggesting a circumtropical distribution).

CYCLOPOID COPEPODS: The copepods Tropocyclops prasinus meridionalis, Ectocyclops rubescens, Mesocyclops aspericornis, and Tropocyclops confinis s.l. all have a circumtropical distribution. The subspecies T. prasinus meridionalis probably deserves to be elevated to species rank. Tropocyclops confinis s.l. is a widely distributed species complex in need of revision. Australoeucyclops aff. timmsi is probably a new

^a *, P < .05; **, P < .01.

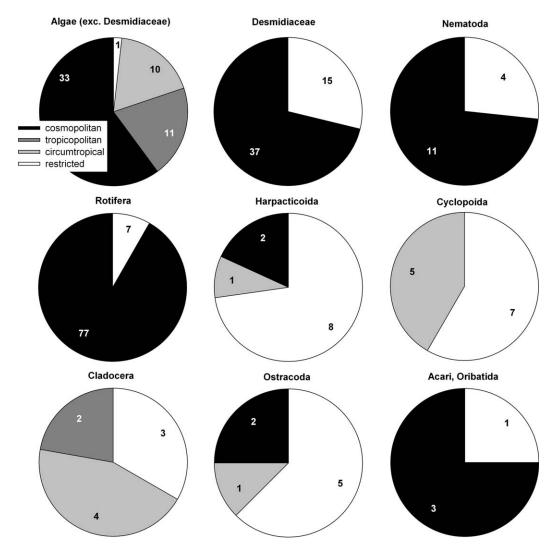


FIGURE 2. Distributions of the major taxonomic groups of organisms. For definitions of the terms "cosmopolitan," "tropicopolitan," "circumtropical," and "restricted" distribution, see the Materials and Methods section. The number of taxa determined to species level is shown in each segment.

taxon; unfortunately Australoeucyclops timmsi was described from New South Wales, Australia (Kiefer 1969), based on females only, and has not been found again. The genus is endemic to Australasia (Karanovič 2004), and so are Mesocyclops woutersi and Thermocyclops crassus macrolasius. The three Mesocyclops aff. woutersi taxa all differ from M. woutersi on the basis of microcharacters whose variability

is still unknown (Holyńska 2000). The two *Microcyclops* aff. *varicans* species differ substantially in the armature of swimming legs but cannot be attributed to any of the described species; the tropical species of this genus too are in urgent need of revision: *Microcyclops varicans* is considered to be cosmopolitan, but several species may be included under this name. More taxonomic effort throughout the

Australasian region is required to define the borders of distribution of the different copepod species.

HARPACTICOID COPEPODS: Nineteen different harpacticoid species belonging to eight families have been found. Members of the families Phyllognathopodidae, Canthocamptidae, and Parastenocarididae are exclusively continental. Diosaccidae, Louriniidae, Cletodidae, and Laophontidae are predominantly marine but have many representatives occurring in brackish (estuarine) environments. The family Ameiridae contains species occurring in marine, brackish, or freshwater environments. In the following paragraphs only the continental representatives are considered.

The genus *Phyllognathopus* is distributed worldwide, but its systematics is confused (Dussart and Defaye 1990) and morphological species discrimination is still lacking (Glatzel and Königshof 2005). The specimens from Cook Islands, Tahiti, and Vanuatu resemble in many aspects the specimens from Western Samoa, identified as *P. viguieri* by Yeatman (1983), and are listed as members of the Australian realm.

Apart from *Mesochra* sp., a globally distributed genus inhabiting estuaries, canthocamptids are represented by two cosmopolitan genera: *Elaphoidella* and *Epactophanes*. *Elaphoidella bidens* shows a worldwide distribution, and *E. sewelli minuta* is only known from central Africa and *Madagascar* (Palaeotropical). *Elaphoidella grandidieri* has a circumtropical distribution and has been found in continental Africa, Asia, South America, and the Caribbean (Dussart and Defaye 1990). Yeatman (1983) reported it, together with *E. taroi*, from Fiji and Western Samoa.

The genus *Epactophanes* has been found on every continent. It has long been considered as monotypic, with *E. richardi*. The confused systematics is comparable with that of *Phyllognathopus* (see Dussart and Defaye 1990). A second species, *E. philippinus*, was recently described from the Philippines and was detected in the samples from Vanuatu, where it cooccurs with an unnamed species. A third, new species was detected on Taveuni, Fiji.

The three representatives of the family Parastenocarididae appear to be directly related to *Parastenocaris leeuweni*, known from high-altitude bryophytes in Sumatra, and with two unnamed *Parastenocaris* species described from Sri Lanka (Enckell 1970) and New Caledonia (Dussart 1984). The three species studied here are considered as faunal elements from the Oriental realm.

CLADOCERANS: Among 33 cladoceran species recorded from Pacific islands by previous authors, only Diaphanosoma samoaensis, recently described from Lac Lanoto'o, Samoa (Korovchinsky 2001), is endemic (Forró et al. 2008). We found it also in a neighboring lake on the island of Upolu (23). Ceriodaphnia cornuta and Ilyocryptus spinifer have a predominantly tropicopolitan distribution; however, "C. cornuta" apparently consists of a group of species (Berner 1985), and *Ilyocryptus spini*fer reaches Nearctic regions in Canada (Kotov and Dumont 2000). Chydorus eurynotus, Diaphanosoma sarsi, and Karualona karua are considered circumtropical (Smirnov 1971, Korovchinsky 2004). Karualona karua also consists of a group of several species with unknown borders of distribution (Dumont and Silva-Briano 2000). Alona setigera has been regarded as Australian, but similar forms have been found in Brazil (Santos-Wisniewski et al. 2001). Bosmina meridionalis is restricted to Australia and New Zealand (Kořínek 1983).

OSTRACODS: With two new genera and three new species the ostracods are the group with the highest level of new taxa (>30%). Limnocythere notodonta has been found in East Africa (McKenzie 1971), and Sarscypridopsis glabrata is known from South Africa (Martens 2001). The new Sarscypridopsis species also have South African affinities (K.M., unpubl. data). More taxonomic research is required to resolve if these are undescribed taxa with a wider distribution or real endemics. The Paracypridinae of Tofua crater lake probably have marine ancestors that overcame the salinity boundary and colonized inland stygohabitats before entering the lake. Cypridopsis vidua and Penthesilenula brasiliensis are cosmopolitan (Martens and Rossetti 2002); Stenocypris major is a circumtropical species (Martens 2001). In concordance with Meisch et al. (2007) we only found female ostracods, implying that all species reproduce parthenogenetically.

oribatid mites: Although most oribatid mites are known as inhabitants of terrestrial habitats, a few taxa are bound to aquatic habitats (Schatz and Behan-Pelletier 2008). All four species of oribatid mites encountered in the material reported here are known to colonize wet and freshwater habitats. Trypochthoniellus longisetus is a cosmopolitan species (excluding Antarctica). Hydrozetes lemnae was found in the Palaearctic, Neotropical, and Oriental regions, as well as in Australia and the Pacific islands. Trimalaconothrus maior has been reported from the Holarctic, western Oriental, and Neotropical regions and New Zealand and the subantarctic islands but not yet from the South Pacific islands. Nasozetes stunkardi is a rare species, which had previously been found only on Guam and the Philippines (Sengbusch 1957). The known distribution of the genus is restricted to the Greater Sunda and the western Pacific islands.

Species Richness

The highest species richness was recorded in high-altitude, fish-free, shallow lakes in the late stage of succession where the basin had silted up and was full of submersed vegetation (12, 13, 25, 32). They were also characterized by comparatively low pH and conductivity. Because we did not specifically sample benthic microhabitats, we introduced a bias toward collecting more tychoplanktonic species in these ecosystems. However, Lake Tagimaucia on Taveuni exhibited by far the highest number of species, although other shallow sites were sampled. In this respect this lake combines several features that are likely to be positively related to species richness: it is situated in the large and geologically old Fiji Archipelago; it is itself relatively old, large, and silted compared with most other investigated crater lakes (minimum of 14,000 yr B.P. [Southern 1986]); and it is close to the Australian continent. In addition the lake is surrounded by diverse swamp vegetation. Within the lake, sedges, mosses, and algae provide a rich mosaic of microhabitats (Southern et al. 1986:509). In contradiction to our results those authors stated that "the fauna of the lake and swamp are low in both diversity and abundance" and that "crustaceans and other invertebrate taxa were scarcely recorded"; however the major focus of that study was on higher plants and animals.

We did not find a significant decrease in species richness with increasing distance of the island from the Australian continent. However, species accumulation curves showed that we sampled no more than 55% of all species present. Each water body was only visited once and different benthic microhabitats were not sampled separately. Hence, additional studies are necessary to obtain a more complete species inventory of South Pacific freshwater ecosystems.

Dispersal

Our survey confirms earlier results from Pacific islands that had revealed impoverished species assemblages with a large proportion of cosmopolitan or circumtropical species and a low level of endemism (Galápagos Islands) or no endemism at all (DeSmet 1989a,b, Segers and Dumont 1993, Dumont and Martens 1996). However, the higher similarity of species communities within archipelagos suggests a more frequent dispersal of freshwater organisms between lakes on the same or between neighboring islands compared with large distance dispersal across the open ocean.

The relatively low number of crustaceans together with a higher proportion of new taxa suggests that viable propagules arrive at a lower rate compared with smaller invertebrates or algae. Endemic species were found, implying that the gene flow between archipelagos is probably low, because of less-effective dispersal abilities, and it may not be frequent enough to overcome local selective pressures. Live resting eggs of calanoid copepods obviously do not reach the South Pacific islands at all, because this group was completely absent from all 39 water bodies.

The relative importance of the different vectors wind, rain, animals, and humans for long-distance dispersal of freshwater invertebrates is still unknown. We can only speculate that the high proportion of small, cosmopolitan taxa in our samples is an indication of arrival by wind and rain. Bohonak and Jenkins (2003) and Bilton et al. (2001) questioned that anemochory and/or ombrochory are important for long-distance dispersal, but Muñoz et al. (2004) found evidence that connection by "wind highways" increases floristic similarities in the Southern Hemisphere. Green and Figuerola (2005) and Frisch et al. (2007) emphasized the importance of migrating birds as vectors. Viable resting eggs of crustaceans have been found attached to feet, bills, and plumage of waterfowl (external phoresis) but also survived transport through the digestive system (internal phoresis). However, the limited number of freshwater habitats on South Pacific islands is not part of major flyways of birds. Some shorebirds are occasionally found near the freshwater sites. They follow the East Asian–Australasian flyway, stretching from Siberia and Alaska, southward through East and Southeast Asia, to Australia and New Zealand. The origin of other vagrant birds (e.g., ducks) is difficult to track down (D. Watling, pers. comm.).

There is a growing list of human-mediated long-distance dispersal of zooplankton species and subsequent establishment of populations (for case studies see Panov et al. [2004]). Humans started to colonize the Pacific islands in a series of waves starting to flow out of East Asia 3,000–4,000 yr ago. The eastern Pacific was reached during the first millennium A.D. (Campbell 2003). Humans imported tools, crops, and animals that could have been contaminated with diapausing stages of freshwater invertebrates. For example, Dumont and Martens (1996) suspected humans as the introducing agent of two crustacean species on Easter Island, which had only been found in the top sediment layers of a crater lake. The abuse of lakes as dumping sites of military equipment during World War II (e.g., Wallis Island) may also have altered species communities. Relatively recently different alien fish species have been introduced into Pacific lakes and ponds and could have carried invertebrate resting eggs in their digestive tracts. Only a systematic survey of sediment cores would shed light on changes of species communities over time.

Threats to Freshwater Communities

Altitude was an important factor in explaining community composition and richness. It was negatively correlated with salt content and probability of fish stocking. Human impact generally decreases with increasing altitude, but we were unable to quantify factors such as habitat degradation within the watershed and nutrient input. However, at this point we anticipate two major threats to freshwater communities, as follows.

(1) Fish Introduction: Of the 39 water bodies investigated, at least 17 had been stocked with nonindigenous fish species. Only three large and deep crater lakes (28, 31, 34) remain unstocked. At least 56 species of freshwater fish have been introduced to the Pacific islands exclusive of the Hawaiian Islands, but not all stocking measures have been successful (Eldredge 2000). Some of these actions date back to the beginning of the last century (e.g., Lake Lanoto'o on Upolu, Samoa, was stocked with goldfish [Carassius auratus] during German occupation). During a campaign in the 1950s to 1970s, tilapias (mostly Oreochromis mossambicus but also O. niloticus, O. aureus, O. urolepis, O. macrochir, Tilapia rendalli, T. zillii, Sarotherodon melanotheron, and S. occidentalis), mosquitofish (Gambusia affinis), and guppies (Poecilia reticulata) were released (Maciolek 1984, Eldredge 2000). Oreochromis mossambicus was the most widely introduced species, having been taken to 19 Pacific island territories, followed by Gambusia affinis (14 territories) and Poecilia reticulata (10 territories).

The main reasons were the provision of an additional source of protein for the local communities and the biological control of mosquitoes. Guppies and swordtails (*Xiphophorus hellerii*, R.S. and G.D., pers. obs. in Lac Vaihiria) probably originated from the aquarium trade and were accidentally or voluntarily released into natural ecosystems. Once populations are established, there is a high risk of contamination of additional

water bodies due to transferral or escape from the point of release.

Today these introduced fish are considered to be pests on Pacific islands. Nevertheless, we witnessed new and illegal stocking of *Tilapia* sp. into lakes in Vanuatu. Their impact on native communities has been detrimental to various groups of animals including native insects (Englund 1999), fish (Lobel 1980), and birds (Stinson et al. 1991, Scott 1993). However, their impact on the native plankton communities of South Pacific lakes has never been studied.

Effects of fish on species richness and community composition were masked by other more prominent variables such as conductivity. However, all introduced fish species are known to develop large populations and prey on a variety of food items at different trophic levels including detritus, algae, and zooplankton (FishBase 2008). Their effect on ecosystem processes is complex (Eby et al. 2006), but direct (predation) and indirect effects (e.g., increased turbidity and loss of microhabitats) may have caused changes in freshwater communities. No systematic monitoring of South Pacific freshwater ecosystems accompanied the large-scale stocking campaign with tilapias and we can only speculate about the impact on the environment. Scott (1993) reported that the originally algal-colored green crater lake on Niuafo'ou, Tonga, lost its color after the introduction of tilapias. Precisely because we know so little about these ecosystems and their invertebrate communities, protecting the remaining lakes from further deterioration is of utmost importance.

(2) Global Warming: We argue that a major threat to South Pacific freshwater ecosystems may arise from global warming and salinization. The Intergovernmental Panel on Climate Change (IPCC) (2007) projected that owing to global warming temperatures will rise by 1.8°C–4.0°C accompanied by a sea level rise of 0.18–0.59 m over the next century. Some of the models also predict more frequent El Niño–Southern Oscillation events (ENSOs), resulting in a 26%–200% increase in rainfall over the central and east-

central Pacific and with possible decreases in the Melanesian and Polynesian regions. Although there is no consensus about the behavior of tropical cyclones in a warmer world, there is reasonable confidence that their intensity is likely to increase by 10%–20% when atmospheric levels of carbon dioxide reach double preindustrial levels as predicted for the end of the twenty-first century (Burns 2002, Hay et al. 2003, Intergovernmental Panel on Climate Change [IPCC] 2007).

Freshwater is a limited resource on most Pacific islands and hence there is great concern about the impact of global warming (Burns 2002, Hay et al. 2003). The basal aquifer on Pacific islands essentially forms a freshwater lens floating on denser salt water (Ghyben-Herzberg lens). Possible scenarios are either that the rising sea level will result in the intrusion of salt water into the freshwater lenses (Watson et al. 1998, White et al. 2007) or, alternatively, that a rise of 40-50 cm might actually increase their volume because the top of the freshwater lens would rise while its base remains relatively unaffected (East-West Center 2001). However, if the rise in sea level is accompanied by coastal erosion together with a reduction in rainfall, the volume of freshwater could be seriously reduced (Burns 2000).

Some of the larger lakes will most likely become important future freshwater reservoirs for humans. Water of Lake Wai Memea (Ambae, Vanuatu) is pumped to the top of the crater rim and provides freshwater for the town of Lolowai (R.S. and G.D., pers. obs.). Further, use of the water of Lake Lanotoʻo on Samoa is being considered to satisfy the growing demand of freshwater in the capital, Apia (T. Tipamaʻa, pers. comm.). However, nothing is known about the limnological conditions in these ecosystems.

There is evidence from our survey for reduced species richness and distinct communities in water bodies experiencing saline intrusions (e.g., 3, 5–11, 17, 30, 34–37) such as the Vais and lakes within the Makatea or the deep crater lakes near sea level. For the latter we assume that freshwater floats on an ion-rich saline and probably hypoxic hypo-

limnion as described in a preliminary study of the remote Tongan lake Vai Lahi on Niuafo'ou island (Maciolek and Yamada 1981).

Rising sea levels, reduced precipitation, potential water removal, and higher frequency of more intense tropical storms could all lead to more intense mixis of the stratified water bodies with a transfer of ion-rich water into the epilimnion. Besides a steady, slow increase in salinity, sudden pulses of salt intrusions into epilimnetic layers seem possible with a potential loss of resilience of the entire ecosystem (Scheffer et al. 2001, Hart et al. 2003). Freshwater plankton communities are sensitive to such saline intrusions (James et al. 2003, Nielsen et al. 2003). As salinity increases, the abundance and species richness of rotifers and microcrustaceans generally decrease (Brock and Shiel 1983, Halse et al. 1998). The threshold for the majority of microzooplankton organisms has been placed at salinities of less than 1-2 ppt (James et al. 2003). Schallenberg et al. (2003) were able to demonstrate severe perturbations of the zooplankton community structure and abundance by even minor saline intrusions just above the range we observed at the surface of Lake Lalolalo and Tofua crater lake.

In their review, Nielsen et al. (2003) stressed the paucity of suitable information for making informed predictions on what future aquatic communities will look like as salinities increase. We therefore suggest launching a monitoring program to assess the stratification and species communities in lakes with various degrees of saltwater intrusions. Long-term data sets should allow scientists to pinpoint species of bioindicative value and provide first predictions on how invertebrate communities might react to water removal and/or saline intrusions. With this information available, these crater lakes could serve as model systems for the detection of salinization, thereby providing Pacific island nations with a warning system for environmental change. Continued ecological and taxonomic research in combination with better management strategies is vital to safeguard the remaining species richness.

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Appendix

Freshwater Algae, Nematoda, Rotifera, Crustacea, and Oribatida Found in South Pacific Freshwater Ecosystems, Their Occurrence in the 39 Investigated Freshwater Ecosystems and Their Known Distribution

Group and Taxa	Site No.	Distribution ^a
Cyanophyceae		
Anabaena cf. spiroides Klebahn, 1895	37	Cosmop.
Aphanizomenon cf. aphanizomenoides (Forti) Hortobágyi	1, 31, 34, 36, 37	Tropicopol.
& Komárek, 1979	1, 21, 21, 20, 27	11opicopon
Aphanocapsa sp.	37	
Aphanothece cf. conglomerata Rich, 1932	37	Circumtrop.
Aphanothece sp.	6, 8, 10, 38	•
Chamaesiphon minutus (Rostafinski) Lemmermann, 1910	34	Cosmop.
Chroococcidiopsis cf. mysorensis Tiwari, 1972	6	Circumtrop.
Chroococcus limneticus Lemmermann, 1898	25, 38	Cosmop.
Chroococcus cf. turgidus (Kützing) Nägeli, 1849	6, 36, 37	Cosmop.
Cyanokybus sp.	34	
Dactylococcopsis irregularis G. M. Smith, 1920	19, 27	Tropicopol.
Heteroleibleinia sp.	34	1 1
Microcystis sp.	6, 7, 8, 9	
Oscillatoria limosa s.l. (Dillwyn) C. Agardh, 1812	25	Cosmop.
Planktolyngbya circumcreta (G. S. West) Anagnostidis &	30	Tropicopol.
Komárek, 1988		1 1
Planktothrix sp.	1, 2, 35	
Pseudanabaena sp.	23, 32	
Radiocystis cf. geminata Skuja, 1948	6, 9	Cosmop.
Dinophyceae	-	1
Gyrodinium sp.	13	
Gymnodinium sp.	13, 26	
Peridinium aciculiferum Lemmermann, 1900	31, 32	Cosmop.
Peridinium africanum var. javanicum (Woloszynska)	1, 12, 13, 15, 16, 19, 20,	Circumtrop.
Lefèvre, 1932	21, 24, 28, 32, 34	r
Peridinium inconspicuum Lemmermann, 1899	1, 4, 12, 13, 15, 16, 22,	Cosmop.
(2 tabulations)	24, 25, 27, 31	
Peridinium cf. lomnickii Woloszynska, 1916	36, 37	Cosmop.
Peridinium sp.	27, 31, 38	
Chrysophyceae		
Synura sp.	32	
Diatomophyceae		
Cyclotella cf. meneghiniana Kützing, 1844	31, 38	Cosmop.
Fragilaria ulna var. acus sensu Lange Bertalot, 1991	31, 32	Cosmop.
Fragilaria sp.	2	
Frustulia sp.	13, 37	
Gyrosigma sp.	37	
Hyalodiscus sp.	35, 36, 37	
Nitzschia sigmoidea (Ehrenberg) W. Smith 1853	13	Cosmop.
Pinnularia sp.	13, 25, 39	
Rhopalodia sp.	10, 33	
Chlorophyceae		
Ankistrodesmus bernardii Komárek, 1983	12, 13, 21, 24, 31	Circumtrop.
Botryococcus sp.	12, 14, 19, 21, 27, 31, 33	1
Chlamydomonas sp.	12, 13	
Coelastrum morus W. West & G. S. West, 1896	13, 15, 16, 27, 31	Tropicopol.
Coelastrum pulchrum Schmidle, 1892	12, 31	Cosmop.
Dictyosphaerium elegans Bachmann, 1933	1, 15, 24, 31, 32	Cosmop.
	14, 16, 19, 20, 22, 24,	Circumtrop.
Dictyosphaerium tetrachotomum Printz var. fallax		I .
Komárek, 1983	31, 32	
Komárek, 1983		Cosmop.
	31, 32 23, 24, 33 18, 23, 32	Cosmop. Cosmop.

Group and Taxa	Site No.	Distribution ^a
Kirchneriella dianae (Bohlin) Comas Gonzalez, 1980	5, 12, 25, 32	Circumtrop.
Lauterborniella sp.	31	•
Monoraphidium komarkovae Nygaard, 1979	22, 34	Cosmop.
Nephrocytium schilleri (Kammerer) Comas González, 1980	19, 24	Tropicopol.
Oocystis lacustris Chodat, 1897	1, 31	Cosmop.
Oonephris palustris Komárek, 1983	12	Circumtrop.
Pandorina morum (O. F. Müller) Bory De Saint- Vincent, 1824	19, 23	Cosmop.
Pediastrum tetras (Ehrenberg) Ralfs, 1844	15, 20, 23	Circumtrop.
Pediastrum simplex Meyen var. biwaense Fukushima, 1956	33	Tropicopol.
Pediastrum duplex Meyen, 1830	33, 37	Cosmop.
Quadricoccus cf. ellipticus Hortobágyi, 1973	32	Tropicopol.
Quadrigula venezuelica Yacubson, 1974	23	Cosmop.
Scenedesmus arcuatus Lemmermann, 1899	31	Cosmop.
Scenedesmus brasiliensis Bohlin, 1897	25	Cosmop.
Scenedesmus javaensis Chodat, 1926	26	Circumtrop.
Scenedesmus perforatus Lemmermann, 1903	12	Circumtrop.
Scenedesmus spinosus Chodat, 1913	38	Cosmop.
Scourfieldia sp.	18	
Tetraedron minimum (A. Braun) Hansgirg, 1888	31	Cosmop.
Trochiscia hystrix (Reinsch) Hansgirg, 1888	12	Europe
Euglenophyceae		
Euglena acus Ehrenberg, 1830	14	Cosmop.
Euglena sp. 1	14, 15, 24, 25, 38	T : 1
Lepocinclis cf. salina F. E. Fritsch, 1914	10, 33	Tropicopol.
Lepocinclis sp.	24, 26	
Phacus sp.	24	C
Phacus curvicauda Svirenko, 1915	14	Cosmop.
Strombomonas maxima (Skvortsov) Deflandre, 1930	26 32	Cosmop.
Trachelomonas hispida (Perty) F. Stein, 1926	32, 33	Cosmop.
Trachelomonas horrida Palmer, 1905	15	Cosmop.
Trachelomonas volvocina Ehrenberg, 1833		Cosmop.
Trachelomonas sp.	2, 7, 9, 24, 32, 33	
Rhodophyceae Audouinella sp.	7	
Compsopogon sp.	35	
Xanthophyceae	33	
Goniochloris fallax Fott, 1960	14, 24	Tropicopol.
Goniochloris sp.	26	торкорої.
Isthmochloron lobulatum (C. Nägeli) H. Skuja, 1948	24	Tropicopol.
Ophiocytium sp.	32	Cosmop.
Pseudostaurastrum limneticum (Borge) Chodat, 1928	32, 33	Tropicopol.
Tetraëdriella sp.	26	торкороі.
Zygnemaphyceae	-0	
Actinotaenium cucurbita (Brébisson) Teiling, 1954	13	Cosmop.
Closterium ceratium Perty, 1852	22	Cosmop.
Closterium calosporum Wittrock	25	Cosmop.
Closterium cynthia De Notaris var. latum (Schmidle) Willi Krieger, 1935	25	Cosmop.
Closterium delpontei (Klebs) Wolle, 1885	13	Cosmop.
Closterium juncidum Ralfs, 1848	13	Cosmop.
Closterium kuetzingii Brébisson, 1856	32	Cosmop.
Closterium lanceolatum Kützing ex Ralfs, 1848	32	Cosmop.
		_ *
Closterium lineatum Ehrenberg ex Ralts, 1848	1.3	COSITIOD:
Closterium lineatum Ehrenberg ex Ralfs, 1848 Closterium navicula (Brébisson) Lütkemüller, 1902	13 13	Cosmop. Cosmop.

Group and Taxa	Site No.	Distribution ^a
Closterium pronum Brébisson, 1856	13	Cosmop.
Cosmarium binum Nordstedt, 1880 in Wittrock and Nordstedt	23, 25	Cosmop.
Cosmarium connatum Brébisson ex Ralfs, 1848	12	Cosmop.
Cosmarium contractum Kirchner var. rotundatum Borge, 1925	13, 22, 23, 25	Cosmop.
Cosmarium cucumis (Corda) ex Ralfs, 1848	24	Cosmop.
Cosmarium depressum (Nägeli) Lundell, 1871	13	Cosmop.
Cosmarium novae-semliae Wille var. sibiricum Boldt, 1885	32	Cosmop.
Cosmarium obsoletum (Hantsch) Reinsch var. sitvense Gutwinski, 1902	28	Indo-Malays.–Nort Aust.
Cosmarium phaseolus Brébisson ex Ralfs var. omphalum (Schaarschmidt) Raciborski, 1889	32	Cosmop.
Cosmarium punctulatum Brébisson var. subpunctulatum (Nordstedt) Børgesen, 1894	13	Cosmop.
Cosmarium retusiforme (Wille) Gutweiler var. incrassatum Gutweiler, 1890	13	Cosmop.
Cosmarium speciosum Lundell, 1871	22	Cosmop.
Euastrum acanthophorum Turner, 1892	13	Indo-Malays.–Nort Aust.
Euastrum ansatum Ehrenberg, 1848	25	Cosmop.
Euastrum didelta Ralfs var. bengalicum Lagerh., 1888	12, 13, 32	Indo-Malays.–Nort Aust.
Euastrum elegans (Brébisson) var. compactum (Wolle) Willi Krieger, 1937	13	Indo-Malays.–Nort Aust.
Euastrum longicolle Nordstedt var. capitatum West & West fa. minus Scott & Prescott, 1958	13	Indo-Malays.–Nort Aust.
Euastrum praemorsum (Nordstedt) Schmidle, 1898	32	Indo-Malays.–Norti Aust.
Euastrum sinuosum Lenorm ex Archer var. parallelum Willi Krieger, 1932	13	Indo-Malays.–Norti Aust.
Euastrum subhexalobum West & West, 1898	13	Indo-Malays.–Nortl Aust.
Euastrum turneri W. West, 1892	13	Cosmop.
Euastrum validum West & West, 1896	32	Indo-Malays.–Norti Aust.
Gonatozygon monotaenium De Bary, 1856	13	Cosmop.
Gonatozygon sp.	28	F
Hyalotheca dissiliens (J. E. Smith) Brébisson ex Ralfs, 1848	13	Cosmop.
Micrasterias anomale Turner, 1892	25	Indo-Malays.–Nort Aust.
Micrasterias rotata Ralfs ex Ralfs, 1848	28	Cosmop.
Micrasterias decemdentata (Nägeli) Archer, 1861	12	Cosmop.
Penium cylindrus (Ehrenberg) ex Brébisson in Ralfs, 1848	13	Cosmop.
Pleurotaenium ehrenbergii (Brébisson) De Bary var. undulatum Schaarschmidt, 1883	13	Cosmop.
Pleurotaenium minutum (Ralfs) Delponte var. gracile (Wille) Willi Krieger, 1932	13	Cosmop.
Pleurotaenium trabecula (Ehrenberg) ex Nägeli var. elongatum Cedergren, 1913	12, 23, 25, 32	Cosmop.
Staurastrum aureolatum Playfair, 1908	13	Aust., New Zealand South Africa
Staurastrum cf. bicorne Hauptfleisch, 1888	13	Cosmop.
Staurastrum cf. controversum Brébisson, 1848	12	Cosmop.
Staurastrum furcatum (Ehrenberg) Brébisson var.	13	Indo-Malays.–Nortl
cercophorum Skuja, 1949		Aust.

Group and Taxa	Site No.	Distribution ^a
Staurastrum leptopus Willi Krieger var. variabile Skuja, 1949	13	Indo-Malays.–North Aust.
Staurastrum punctulatum Brébisson ex Ralfs, 1848	12	Cosmop.
Staurastrum sexangulare (Bulnheim) P. Lundell var. subglabrum West & West, 1902	13	Indo-Malays.–North Aust.
Staurastrum sp.	32	
Staurodesmus connatus (P. Lundell) Thomasson, 1960	13	Cosmop.
Staurodesmus glaber (Ehrenberg ex Ralfs) Teiling, 1948	12	Cosmop.
Tetmemorus laevis (Kützing) Ralfs var. tropicus Willi Krieger, 1937	13	Indo-Malays.–North Aust.
Nematoda		
Achromadora pseudomicoletzkyi Van Der Linde, 1938	3	Cosmop.
Achromadora cf. tenax (De Man, 1876)	12	Cosmop.
Achromadora sp.	3, 25	1
Aphelenchoides sp. 1	3, 9, 34	
Aphelenchoides sp. 2	3	
Aphelenchoides sp. 3	9	
Araeolaimus sp.	34	
Cobbonchus sp.	28	
Dichromadora cf. tobaensis Schneider, 1937	34, 36	Sumatra
Eudorylaimus sp.	26	
Eumonbystera dispar (Bastian, 1865)	2	Cosmop.
Eumonhystera vulgaris (De Man, 1880)	13, 25	Cosmop.
Eumonbystera sp. 1	2	
Eumonhystera sp. 2	2	
Eumonhystera sp. 3	12	
Eutobrilus sp.	12, 26, 31	_
Ironus cf. longicaudatus De Man, 1884	2, 28	Cosmop.
Ironus cf. tenuicaudatus (De Man, 1876)	12	Cosmop.
Mesodorylaimus cf. guarani Andrássy, 1968	13	Paraguay, Costa Rica
Mesodorylaimus cf. meyli (Andrássy, 1958)	1, 9, 15, 19, 26, 32, 34, 37, 38, 39	Europe, Russia, Tadzhikistan
Mesodorylaimus sp. 1	1	
Mesodorylaimus sp. 2	13	
Mononchus aquaticus Coetzee, 1968	20, 33	Cosmop.
Mylonchulus cf. lacustris (Cobb, 1915)	1, 4, 28	Cosmop.
Myolaimus heterurus Cobb, 1920	3	Cosmop.
Neoactinolaimus cf. duplicidentatus (Andrássy, 1968)	13, 22, 23	Europe, Congo, USA Venezuela
Oncholaimus cf. oxyuris Ditlevsen, 1911	37	Cosmop.
Oncholaimus cf. skawensis Ditlevsen, 1921	36, 37, 38	Cosmop.
Panagrolaimus sp.	26	
Plectus sp.	2, 26	
Pratylenchidae	8	
Rhabditidae	11	
Tobrilus sp. 1	2, 4, 25, 26	
Tobrilus sp. 2	24	
Tylenchidae	9	
Xiphinema sp.	8	
Rotifera	12 15 16 10 20 22	
Anuraeopsis fissa Gosse, 1851	13, 15, 16, 19, 20, 22, 23, 28, 32, 34	Cosmop.
Anuraeopsis navicula Rousselet, 1911	21, 24, 31, 33	Pres. Cosmop.
Ascomporpha saltans indica Wulfert, 1966	12	Pres. Cosmop.
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Ascomorpha saltans saltans Bartsch, 1870	15, 16, 19	Cosmop.
	15, 16, 19 13	Cosmop.

roup and Taxa	Site No.	Distribution ^a
Beauchampiella eudactylota (Gosse, 1886)	25	Cosmop.
Brachionus plicatilis Müller, 1786	38	Cosmop.
Brachionus quadridentatus f. cluniorbicularis Skorikov, 1894	26, 27	Cosmop.
Brachionus quadridentatus melhemi Barrois & Daday, 1894	23	Pres. Cosmop.
Brachionus quadridentatus quadridentatus Hermann, 1783	15, 21, 22, 24, 33	Cosmop.
Brachionus urceolaris Müller, 1773	34	Cosmop.
Cephalodella forficula (Ehrenberg, 1830)	12, 26, 33	Cosmop.
Cephalodella gibba (Ehrenberg, 1830)	2, 12, 39	Cosmop.
Cephalodella gracilis (Ehrenberg, 1830)	4	Pres. Cosmop.
Cephalodella cf. incila Wulfert, 1937	39	Holarctic, Pacific
Cephalodella intuta Myers, 1924	13	Cosmop.
_ *		Cosmop.
Cephalodella spp.	2, 4, 12, 13, 22, 39	
Collotheca sp.	12, 13, 28	Coomon
Columella adriatica Ehrenberg, 1831	35, 36, 38, 39	Cosmop.
Colurella obtusa (Gosse, 1886)	2, 27, 31, 34, 39	Cosmop.
Colurella uncinata (Müller, 1773)	13, 39	Cosmop.
Colurella uncinata f. bicuspidata (Ehrenberg, 1830)	32, 39	Cosmop.
Colurella sp.	3, 15, 33	0
Dicranophorus epicharis Harring & Myers, 1928	1, 2, 4, 26	Cosmop.
Dicranophorus cf. grandis (Ehrenberg, 1832)	39	Cosmop.
Epiphanes brachionus var. spinosa (Rousselet, 1901)	16, 17	Pres. Cosmop.
Euchlanis dilatata Ehrenberg, 1832	31, 32	Cosmop.
Euchlanis incisa Carlin, 1939	13	Cosmop.
Filinia saltator (Gosse, 1886)	19, 20	Pres. Cosmop.
Hexarthra brandorffi Koste, 1977	1, 17	Western Hemisphe
Hexarthra cf. fennica (Levander, 1892)	10, 31, 34, 38	Pres. Cosmop.
Hexarthra oxyuris (Zernov, 1903)	36, 37	Cosmop.
Keratella procurva (Thorpe, 1891)	28	Cosmop.
Lecane aculeata (Jakubski, 1912)	27, 34	Pres. Cosmop.
Lecane arcuata (Bryce, 1891)	2	Cosmop.
Lecane arcula Harring, 1914	2, 12, 13	Cosmop.
Lecane bifurca (Bryce, 1892)	39	Cosmop.
Lecane bulla (Gosse, 1851)	12, 13, 15, 22, 25, 26, 27,	Cosmop.
Lecane closterocerca (Schmarda, 1859)	28, 31, 32, 34, 37, 39 2, 3, 4, 7, 11, 13, 26, 27, 28, 38, 39	Cosmop.
Lecane cf. doryssa Harring, 1914	13	Pres. Cosmop.
Lecane flexilis (Gosse, 1886)	28	Cosmop.
Lecane furcata (Murray, 1913)	1, 2, 32	Cosmop.
Lecane haliclysta Harring & Myers, 1926	28	Cosmop.
Lecane bamata (Stokes, 1896)	2, 3, 4, 22, 24, 26, 27, 28, 31, 32, 39	Cosmop.
Lecane hornemanni (Ehrenberg, 1834)	13	Cosmop.
Lecane inermis (Bryce, 1892)	4, 11, 31, 39	Cosmop.
Lecane ludwigii (Eckstein, 1883)	13	Cosmop.
Lecane luna (Müller, 1776)	2	Cosmop.
Lecane lunaris (Ehrenberg, 1832)	12, 13	Cosmop.
Lecane monostyla (Daday, 1897)	2, 4, 13	Cosmop.
Lecane nana (Murray, 1913)	26	Cosmop.
Lecane obtusa (Murray, 1913)	38	Orient.
Lecane papuana (Murray, 1913)	33, 39	Cosmop.
Lecane paxiana Hauer, 1940	2	Eastern Hemispher
Lecane plesia Myers, 1936	35	Pres. Cosmop.
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roup and Taxa	Site No.	Distribution ^a
Lecane pusilla Harring, 1914	13, 27, 31	Pres. Cosmop.
Lecane pyriformis (Daday, 1905)	1, 2, 4, 8, 9, 12, 13, 26, 27, 34, 39	Cosmop.
Lecane cf. rhytida Harring & Myers, 1926	28	Pres. Cosmop.
Lecane robertsonae Segers, 1993	2	Orient., Aust., Neotroj
Lecane signifera ploenensis (Voigt, 1902)	13	Cosmop.
Lecane undulata Hauer, 1938	18, 26	Cosmop.
Lecane tenuiseta Harring, 1914	3, 18, 26	Cosmop.
Lecane thalera (Harring & Myers, 1926)	6	Pres. Cosmop.
Lepadella acuminata (Ehrenberg, 1834)	1, 39	Cosmop.
Lepadella apsicora Myers, 1934	12, 15, 22, 25	Pres. Cosmop.
Lepadella desmeti Segers & Chittapun, 2001	26	Orient., Aust., Neotroj
Lepadella patella (Müller, 1773)	1, 2, 3, 4, 39	Cosmop.
Lepadella patella persimilis De Ridder, 1961	34	Cosmop.
Lepadella rhomboides (Gosse, 1886)	15, 20, 27	Cosmop.
Lepadella sp. near costatoides Segers, 1992	26, 27	Cosmop.
Lepadella sp.	4, 31	-
Lepadella triba Myers, 1934	4	Cosmop.
Lepadella triptera (Ehrenberg, 1832)	32	Cosmop.
Monommata maculata Harring & Myers, 1930	13	Cosmop.
Mytilina ventralis var. macracantha (Gosse, 1886)	1, 32	Cosmop.
Notommata cf. allantois/pachyura	2	
Plationus patulus patulus (Müller, 1786)	12, 13, 32	Cosmop.
Polyarthra indica Segers & Babu, 1999	13, 15, 16, 17, 19, 21, 22, 23, 24, 25, 32, 33	Africa, Orient.
Polyarthra cf. vulgaris Carlin, 1943	32	Cosmop.
Polyarthra sp.	13	•
Proalinopsis sp.	12	
Ptygura sp.	13, 28, 34	
Scaridium sp.	12	
Squatinella sp.	26	
Testudinella incisa (Ternetz, 1892)	13	Cosmop.
Testudinella patina (Hermann, 1783)	13, 31, 34	Cosmop.
Trichocerca bidens (Lucks, 1912)	12, 13	Cosmop.
Trichocerca chattoni (De Beauchamp, 1907)	15, 20	Pres. Cosmop.
Trichocerca pusilla (Jennings, 1903)	15, 21, 22, 24, 26, 27, 32	Cosmop.
Trichocerca cf. similis (Wierzejski, 1893)	13, 21, 24, 32	Cosmop.
Trichocerca tenuior (Gosse, 1886)	1, 2, 16, 19, 26, 39	Cosmop.
Trichocerca weberi (Jennings, 1903)	22, 32	Cosmop.
Trichocerca sp.	20	
Trichotria tetractis tetractis (Ehrenberg, 1830)	13	Cosmop.
Bdelloidea gen. spp.	1, 3, 4, 5, 7, 9, 10, 11, 16, 17, 20, 33, 39	
yclopoida	10, 17, 20, 33, 37	
Australoeucyclops aff. timmsi Kiefer, 1969	12	Australasian
Ectocyclops rubescens Brady, 1904	13	Circumtrop.
Halicyclops sp.	36	
Mesocyclops aspericornis (Daday, 1906)	5, 6, 10, 17, 19	Circumtrop.
Mesocyclops woutersi Van De Felde, 1987	31	Australasian
Mesocyclops sp. 1 aff. woutersi Van De Felde, 1987	1, 2	Endemic?
Mesocyclops sp. 2 aff. woutersi Van De Felde, 1987	18, 30	Endemic?
Mesocyclops sp. 3 aff. woutersi Van De Felde, 1987	14	Endemic?
Microcyclops sp. 1 aff. varicans (Sars, 1863)	1, 32, 34	Endemic?
Microcyclops sp. 2 aff. varicans (Sars, 1863)	21, 25	Circumtrop.?
Thermocyclops crassus macrolasius Kiefer, 1952	27, 28, 31, 33	Australasian
Tropocyclops confinis s.l. Kiefer, 1930	13, 24, 25	Circumtrop.

Group and Taxa	Site No.	Distribution ^a
Tropocyclops prasinus meridionalis Kiefer, 1931	13	Circumtrop.
Unidentifiable copepodids	3, 7, 11, 15, 16, 20, 37	•
Harpacticoida		
Amphiascus sp.	35	(Marine-estuarine)
Elaphoidella cf. bidens (Schmeil, 1894)	13, 23	Cosmop.
Elaphoidella grandidieri (Guerne & Richard, 1893)	7, 13, 23, 25	Circumtrop.
Elaphoidella "sewelli/minuta"	22, 23	Palaeotrop.
Epactophanes philippinus Bruno & Cottarelli, 1999	28	Palaeotrop.
Epactophanes sp. 1	28	Orient.
Epactophanes sp. 2	13	Orient.
Limnocletodes sp.	3	(Marine-estuarine)
Lourinia armata (Claus, 1866)	35	(Marine-estuarine)
Nitocra "lacustris group"	7, 8, 13, 34, 35, 36, 37	Cosmop.
Mesochra sp.	7	(Marine–estuarine)
Onychocamptus mohammed (Blanchard & Richard, 1891)	38	(Marine-estuarine)
Parastenocaris sp. 1	28	Palaeotrop.
Parastenocaris sp. 2	28	Palaeotrop.
Parastenocaris sp. 3	13, 28	Palaeotrop.
Phyllognathopus sp.	2, 7, 26	Aust.
Schizopera cf. tobae Chappuis, 1931	10	(Marine–estuarine)
Schizopera sp. 1	6, 7, 37	(Marine–estuarine)
Xanthiphonte sp.	35	(Marine–estuarine)
Cladocera		(171111111 Coccuminate)
Alona setigera Brehm, 1931	28	Aust.?
Bosmina cf. meridionalis Sars, 1904	1	Aust., New Zealand
Ceriodaphnia cornuta Sars, 1885	15, 17	Tropicopol.
Chydorus eurynotus Sars, 1901	12, 13, 32	Circumtrop.
Diaphanosoma samoaensis Korovchinsky, 2001	21, 23	Endemic (Samoa)
Diaphanosoma sarsi Richard, 1894	13, 31, 32	Circumtrop.
Ilyocryptus spinifer Herrick, 1882	25	Tropicopol.
Karualona karua (King, 1853)	13	Circumtrop.
Macrothrix spinosa King, 1853	12, 13, 25	Circumtrop.
Ostracoda	12, 13, 23	Gircuma op.
Cypridopsis vidua (O. F. Müller, 1776)	1, 7, 31, 34	Cosmop.
Cypridopsinae n. gen., n. sp.	34	New
Limnocythere notodonta Vávra, 1906	12, 34	East Africa
Paracypridinae gen. and sp. unident.	35	East Milea
Penthesilenula brasiliensis (Pinto & Kotzian, 1961)	3	Cosmop.
Sarscypridopsis cf. glabrata (Sars, 1924)	19	South Africa
Sarscypridopsis n. sp. 1	8	New
Sarscypridopsis n. sp. 1 Sarscypridopsis n. gen, n. sp. 2	32, 33	New
Stenocypris major (Baird, 1859)	4, 19, 31, 34	Circumtrop.
Ostracoda gen. spp.	4, 6, 7, 12, 13, 22, 28	Circuma op.
Acari: Oribatida	1, 0, 7, 12, 13, 22, 20	
Hydrozetes lemnae (Coggi, 1899)	12, 13	Palaearct., Neotrop.,
Tryurozetts umnut (Coggi, 1077)	12, 19	Aust., Orient., Pacific
Nasozetes stunkardi Sengbusch, 1957	13	Guam, Philippines
Trhypochthoniellus longisetus (Berlese, 1910)	25	Cosmop. exc.
1 raypotationicuus ungistius (Bellese, 1/10)	23	Antarctica
Trimalaconothrus maior (Berlese, 1910)	1, 8, 10, 13, 18, 25, 34	Hitarctica Holarctic, western Orient., Neotrop., New Zealand, subantarctic islands

[&]quot;Cosmop., cosmopolitan (at least six major biogeographic regions [not including Pacific or Antarctic regions]); Circumtrop., circumtropical; Tropicopol., tropicopolitan; Palaeotrop., Palaeotropic; Aust., Australian; Orient., Oriental; Afrotrop., Afrotropic; Palaearct., Palaearctic; Neotrop., Neotropic; Pres. Cosmop., presumed cosmopolitan (at least four major biogeographic regions, including at least one in the New World).