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Freshwater lakes of Ulu Peninsula, James Ross Island, north-east Antarctic Peninsula: origin, geomorphology and physical and chemical limnology

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Abstract: This study describes the origin, bedrock geology, geomorphology, hydrological stability and physical and chemical characteristics of a representative set of 29 lakes in the ice-free parts of the Ulu Peninsula, James Ross Island, located close to the northern tip of the Antarctic Peninsula. Based on these features, six different types of lakes were defined: stable shallow lakes on higher-altitude levelled surfaces, shallow coastal lakes, stable lakes in old moraines, small unstable lakes in young moraines, deep cirque lakes and kettle lakes. We observed a significant relationship between lake type and water chemistry. Bedrock, lake age and morphometry together with altitude were the most important factors underlying the observed limnological variability. Our results further suggested possible nitrogen limitation in the lake ecosystems. However, physical factors such as low temperature and light were also likely to be limiting.

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Key words: conductivity, deglaciation, lake origin, lake types, morphometry, nutrients

Introduction

Although the Antarctic continent is almost completely covered by an ice sheet, one of its characteristic features is a surprising diversity and abundance of lakes. Besides subglacial lakes (Siegert *et al*. 2005), the majority of them are situated in coastal oases in continental Antarctica such as the McMurdo Dry Valleys, Vestfold Hills, Larseman Hills, Bunger Hills, Syowa Oasis and Schirmacher Oasis (Verleyen *et al*. 2012). However, many ice-free areas with lakes can also be found on the Antarctic Peninsula and surrounding islands. These lakes mostly occupy depressions created by glacial erosion and were formed following Holocene ice sheet retreat (Vincent & Laybourn-Parry 2008), or isostatic uplift (e.g. Roberts *et al*. 2011). Limnological surveys of freshwater lakes in this region have been carried out, for example, on the South Shetland Islands (Toro *et al*. 2007), and on Beak Island (Sterken *et al*. 2012) and they have shown a wide range of limnological conditions with nutrient status ranging from ultraoligotrophic to eutrophic.

The Antarctic Peninsula has been identified as one of the most rapidly warming parts of our planet during the last 50 years (Vaughan *et al*. 2003). There is growing evidence that Antarctic lakes are sensitive indicators of climate change (Quayle *et al*. 2002) as well as being valuable centres of biodiversity (Vincent & Laybourn-Parry 2008). However, lake distribution, their physical and chemical characteristics, and biology are generally poorly known around the Antarctic Peninsula. Additional studies are thus needed to complete our knowledge of the current limnological diversity in this part of Antarctica.

James Ross Island belongs to a transitory zone between the maritime Antarctic and continental Antarctic regions. More than 80% of the island surface is covered with ice. Only the northernmost part of the island, the Ulu Peninsula, is significantly deglaciated and represents one of the largest ice-free areas (oasis) in the northern part of the Antarctic Peninsula. Multiple glaciation of the island with ice streaming from James Ross Island and the Antarctic Peninsula has resulted in deeply incised glacial valleys, which lie partly on land and are partly flooded by the sea at present (Nývlt *et al*. 2011). The origin of the lakes on James Ross Island is related to the last deglaciation of the Antarctic Peninsula ice sheet and the retreat of the James Ross Island ice cap during the Late Glacial (Nývlt, unpublished data) and the Holocene, and to relative sea level changes resulting from postglacial isostatic recovery (Hjort *et al*. 1997).

Interaction between volcanic landforms and glacial geomorphology during previous glacial-interglacial cycles and Holocene paraglacial and periglacial processes and relative sea level change has resulted in the complex

Table I. Location and main characteristics of the James Ross Island lakes and their catchments.

Lake	Code	GPS S	GPS W	Type	Altitude m a.s.l.	Bedrock	Catchment area (without mesas) m^2	Lake area m^2	Shore line m	Length m	Max. breadth m	Development of shore line	Vol. m^3	Max. depth m	Mean depth m	Development of volume	Relative depth %
Argentino	ARG	63°54'52.7"	57°56 36.4"	6	216	M	ND	15 160	474	157	143	1.09	ND	ND	ND	ND	ND
Bibby	BIB	63°49'10.1"	57°55 48.1"	4	250	M	48 700	7439	515	209	52	1.68	7880	2.7	1.1	0.39	2.77
Black	BLA	63°57'58.1"	57°52 59.7"	1	166	V	61 756	5363	301	108	77	1.16	1135	0.5	0.2	0.47	0.54
Blue-green	BLU	63°54'54.2"	57°57 24.6"	6	184	M	ND	3806	303	115	48	1.39	ND	ND	ND	ND	ND
Cyanobacterial	CYA	63°57'56.4"	57°54 25.0"	1	185	V	299 861	6944	466	137	84	1.58	4510	1.5	0.6	0.4	1.6
Dan	DAN	63°52'44.0"	57°58 43.8"	3	41	C	1 597 449	13 280	547	191	103	1.34	1418	0.2	0.1	0.46	0.18
Federico	FED	63°56'16.5"	57°58'50.2"	4	387	M	67 885	8269	438	137	88	1.36	ND	ND	ND	ND	ND
Ginger	GIN	63°52'29.4"	57°48'10.2"	6	197	M	ND	12 170	532	222	96	1.36	ND	ND	ND	ND	ND
Green 1	GR1	63°54'11.7"	57°46'49.9"	1	65	V	340 515	4220	324	140	40	1.41	2183	1.1	0.5	0.49	1.43
Green 2	GR2	63°53'54.6"	57°46'33.8"	1	40	V	368 586	2970	214	79	56	1.11	1037	0.9	0.3	0.39	1.46
Katia 1	KA1	63°52'23.1"	57°58'32.7"	3	36	C	84 783	3289	282	87	58	1.39	716	0.5	0.2	0.46	0.73
Katia 2	KA2	63°52'15.9"	57°58'32.5"	3	38	C	131 953	1518	194	80	30	1.4	195	0.3	0.1	0.49	0.59
Lachman 1	LA1	63°47'34.9"	57°48'13.8"	2	9	G	394 209	29 670	1267	598	85	2.07	4754	0.3	0.2	0.53	0.15
Lachman 2	LA2	63°47'59.9"	57°48'31.1"	2	13	G	200 187	14 670	635	264	76	1.48	1871	0.4	0.1	0.36	0.26
Láska	LAS	63°49'25.4"	57°50'41.3"	6	269	M	ND	1455	163	58	33	1.21	1824	3.8	1.3	0.33	8.83
Monolith	MON	63°53'52.3"	57°57'29.0"	3	67	C+G	1 886 055	93 050	1351	439	295	1.25	116 600	2.2	1.3	0.57	0.64
Muddy	MUD	63°51'50.1"	57°57'12.2"	2	4	C	425 356	10 940	427	162	105	1.15	ND	ND	ND	ND	ND
Naděje	NAD	63°48'51.9"	57°50'05.6"	5	236	M	91 752	8147	444	160	67	1.39	45 050	12	5.5	0.46	11.78
Omega 1	OM1	62°51'40.0"	57°48'50.0"	6	257	M	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
Omega 2	OM2	63°51'59.0"	57°47'37.9"	6	153	M	ND	16 490	663	209	144	1.46	99 000	10.9	6	0.55	7.52
Phormidium	PHO	63°50'48.6"	58°00'28.1"	3	10	C+G	9 146 393	158 100	2495	1030	276	1.77	18 220	0.3	0.1	0.34	0.08
Red	RED	63°54'33.3"	57°47'46.3"	1	65	V	129 386	4324	254	100	60	1.09	2072	1.1	0.5	0.44	1.48
Rožmberk	RO1	63°49'03.8"	57°50'43.7"	5	201	M	195 347	88 390	1222	431	330	1.16	1 580 000	32.5	17.9	0.55	9.69
Rozkoš	RO2	63°49'22.7"	57°50'41.1"	6	260	M	ND	1944	171	55	48	1.09	5120	4.6	2.6	0.57	9.25
Vondra 1	VO1	63°57'40.7"	57°54'10.2"	1	229	V	54 057	18 050	550	221	115	1.15	27 790	3.5	1.5	0.44	2.31
Vondra 2	VO2	63°57'36.3"	57°54'22.7"	1	228	V	77 759	5977	312	124	73	1.14	8270	3.9	1.4	0.35	4.47
Vondra 3	VO3	63°57'33.4"	57°54'08.3"	1	235	V	43 563	13 300	450	153	118	1.1	18 020	3.1	1.4	0.44	2.38
Vondra 4	VO4	63°57'37.1"	57°53'54.8"	1	221	V	109 619	6077	361	153	52	1.31	8750	3.4	1.4	0.42	3.87
White	WHI	63°53'49.7"	57°48'44.7"	1	65	V	380 112	6662	353	146	63	1.22	4915	1.8	0.7	0.41	1.95

Bedrock explanation: C = Late Cretaceous marine sediments, G = Miocene–Holocene glacial sediments composed mostly of local volcanic rocks and marine Cretaceous sediments, with minor admixture of Antarctic Peninsula derived igneous and metamorphic rocks, M = recent glacigenic (morainic) sediments with present glacier ice composed mostly of local volcanic rocks, with some admixture of marine Cretaceous sediments, V = Neogene volcanic rocks consisting mostly of hyaloclastite breccias, tuffs and subaerial basalts.

ND = not determined.

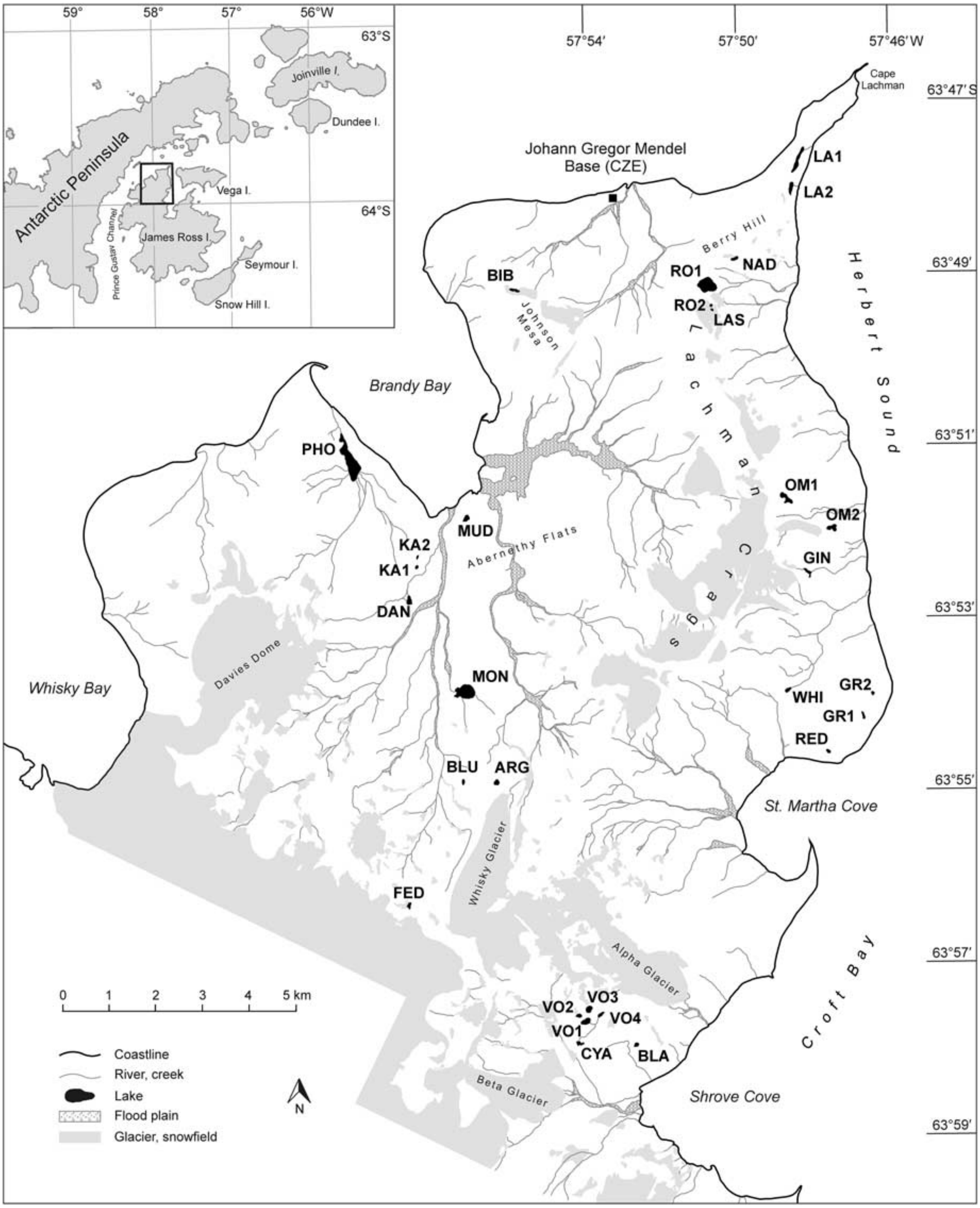

Fig. 1. Detailed map of the Ulu Peninsula showing the location of lakes sampled in 2008–09. The inset map shows the tip of the Antarctic Peninsula with the position of James Ross Island and the Ulu Peninsula. Topography based on a map by the Czech Geological Survey (CGS 2009). For lake codes, see Table I.

present-day landscape of James Ross Island (Davies *et al.* in press). All of these processes have influenced the development of the lakes which are found on the Ulu Peninsula at altitudes ranging from < 20 m above sea level (a.s.l.) near the coast to *c.* 400 m a.s.l. in the mountain areas.

Until now, the study of lakes on James Ross Island has been mostly limited to palaeolimnological investigations. A detailed description of sediment profiles sampled from lakes in Brandy Bay (including Monolith Lake) resulted in the reconstruction of climate changes in the area spanning

Table II. Methods used for the determination of chemical composition of lakes.

Abbreviation	Explanation	Assessment
TC, DC	Total and dissolved organic C	TOC/TN analyzer (Formacs)
PC	Particulate C	PC = PTC – DC
DOC	Dissolved organic C	TOC 5000A analyzer (Shimadzu)
TN, DN	Total and dissolved N	TOC/TN analyzer (Formacs)
PN	Particulate N	PN = TN – DN
DON	Dissolved organic N	DON = DN – NO_3-N – NO_2-N – NH_4-N
TP, DP	Total and dissolved P	$HClO_4$ digestion and molybdate method (Kopáček & Hejzlar 1993)
PP	Particulate P	PP = TP – DP
SRP	Dissolved reactive P	Molybdate method (Murphy & Riley 1962)
Si	Dissolved Si	Molybdate method (Golterman & Clymo 1969)
NH_4^+, NO_3^-, Cl^-, SO_4^{2-}, F^-, Ca^{2+}, Mg^{2+}, Na^+, K^+		Dionex IC25, USA
Fe, Mn		Atomic absorption spectroscopy (Varian)
NO_2^-		Bendschneider & Robinson (1952)

TOC = total organic carbon.

the last 5000 years (Björck *et al.* 1996). However, information about the recent limnological status of the lakes is limited to several temperature, pH and conductivity measurements recorded during investigations of their cyanobacterial microflora (Komárek & Elster 2008).

The aim of this paper is to describe in detail the lake types found on the Ulu Peninsula, their origin, age, morphometry, and physical and chemical characteristics. The results of this study can serve as baseline information for future limnological investigations in the region of the Antarctic Peninsula, and also for biological assessments of the lakes.

Materials and methods

Study area

James Ross Island (64°10'S, 57°45'W) is a *c.* 2600 km^2 large island situated in the north-western part of the Weddell Sea, close to the northern tip of the Antarctic Peninsula. The climate is characterized by short summers (December–February) when the mean monthly air temperature exceeds 0°C. The annual mean temperature at the Mendel station close to sea level is -6.6°C (2004–09; K. Láska, personal communication 2012). Compared to the South Shetland Islands on the western side of the Antarctic Peninsula, James Ross Island is more arid (Aristarain *et al.* 1987). The terrestrial vegetation on the island is limited to non-vascular plants and composed of a predominantly bryophyte and lichen tundra. Human presence is limited to the northern side of the island, where the Czech Johann Gregor Mendel Antarctic research station has been located since 2006. Seasonal Argentinean and British field camps have been established at various locations on the deglaciated part of the Ulu Peninsula during the last five decades, typically located close to water sources such as Phormidium, Monolith, or Lachman lakes.

Deglaciation in this area began before 12.9 ka (Nývlt, unpublished data) and lower-lying areas of the Ulu Peninsula were ice-free at the beginning of the Holocene. A glacially levelled surface, which is synchronous with the Late Glacial deglaciation event, lies at *c.* 50 m a.s.l. and may be traced along the north-western slope of Berry Hill and at Cape Lachman (Nývlt, unpublished data). However, advances of individual local glaciers are known to have occurred during the Holocene (Björck *et al.* 1996, Hjort *et al.* 1997, Carrivick *et al.* in press). Evidence for this includes moraine ridges in Brandy Bay (Hjort *et al.* 1997, Davies *et al.* in press) and vast debris-covered glaciers or rock glaciers along the eastern side of the Lachman Crags Mesa (Fukui *et al.* 2008). Only small glaciers are present in the northern part of the Ulu Peninsula at present (cf. CGS 2009, Engel *et al.* 2012). They mostly represent remnants of former larger neoglacial glaciers and their retreat has been detected both from remote sensing data, and in the field (Carrivick *et al.* in press).

Rapid deglaciation during the Late Glacial and earliest Holocene resulted in the formation of marine terraces (Hjort *et al.* 1997). The highest late Quaternary marine terrace, which lies at *c.* 30 m a.s.l., was 'tentatively' dated by Hjort *et al.* (1997) at *c.* 8560 ± 100 ^{14}C yr BP. Remnants of this marine level may be found south of St. Martha Cove, near the Mendel station, and in the Abernethy Flats. A further prominent Holocene terrace at *c.* 16 m a.s.l. described by Hjort *et al.* (1997) is well preserved at the neck of Cape Lachman (Nývlt, unpublished data), in Abernethy Flats and in the Phormidium Lake area. The younger marine terraces found at *c.* 8 and *c.* 4 m a.s.l. have not been dated so far, but they probably represent late Holocene sea levels. Similar relative sea level changes have been recorded by Roberts *et al.* (2011) for Beak Island, which is located $<$ 50 km north-east of the Ulu Peninsula. On the basis of this study, the 'tentative marine limit of 30 m' of Hjort *et al.* (1997) at 8560 ± 100 ^{14}C yr BP (8131 cal. yr BP) was reinterpreted as an earlier Quaternary marine limit. The well developed beach ridges up to 18 m a.s.l. at Comb Ridge on The Naze (Hjort *et al.* 1997), which correspond with a marine terrace at *c.* 16 m a.s.l. at Cape Lachman, in Abernethy Flats and in the Phormidium Lake area, are probably the Late Glacial to

Table III. Physical and chemical characteristics of the lakes.

Code	Date	Temp. °C	O_2 mg l^{-1}	pH	ANC mmol l^{-1}	Conductivity (25°C) µS cm^{-1}	Na^+ mg l^{-1}	K^+ mg l^{-1}	Ca^{2+} mg l^{-1}	Mg^{2+} mg l^{-1}	SO_4^{2-} mg l^{-1}	Cl^- mg l^{-1}	NO_3-N µg l^{-1}	NO_2-N µg l^{-1}	NH_4-N µg l^{-1}	DON µg l^{-1}	PN µg l^{-1}	DP µg l^{-1}	PP µg l^{-1}	SRP µg l^{-1}	DOC mg l^{-1}	PC mg l^{-1}	Si mg l^{-1}
ARG	27/01/2009	1.0	16.9	7.6	562	91	15.7	0.35	3.03	0.54	10.1	3.27	37	0.8	< 5	124	62	49.0	78.0	45.4	0.45	0.39	1.01
BIB	25/02/2008	13.0	10.6	6.8	65	25	6.4	0.33	0.54	0.27	1.93	7.79	< 5	0.8	< 5	88	ND	28.0	7.7	27.5	0.42	0.03	0.15
BLA	19/01/2009	8.3	12.0	7.9	751	130	11.5	0.7	7.01	4.47	2.5	14.8	6	0.2	107	383	114	7.6	6.0	3.6	5.14	2.53	2.2
BLU	27/01/2009	5.5	16.4	7.8	698	91	10.3	0.42	5.2	0.74	2.63	4.06	18	0.4	< 5	164	62	63.0	16.0	54.5	0.82	1.87	1.29
CYA	19/01/2009	7.1	13.2	8.7	884	99	15.6	0.51	4.9	1.03	2.46	3.52	10	0.5	< 5	193	104	65.0	21.0	54.9	1.3	0.99	2.96
DAN	02/02/2008	9.8	13.4	7.6	412	141	11.4	0.23	15.4	2.86	44.8	4.86	< 5	1.1	< 5	120	ND	4.6	4.0	2.2	1.45	0.26	1.11
FED	27/01/2009	0.3	23.0	9.5	382	78	13.7	0.22	0.9	0.22	3.22	7.03	13	1.5	< 5	317	52	71.0	24.0	64.2	1.68	0.84	1.94
GIN	15/01/2009	ND	11.5	7.2	180	33	5.1	0.19	0.63	0.4	1.06	3.29	60	0.1	7	118	52	64.0	24.0	63.0	0.68	3.35	0.18
GR1	22/02/2008	9.4	11.6	7.2	236	55	4.7	0.24	2.12	1.24	1.74	5.25	< 5	0.6	6	161	20	7.8	4.6	4.0	1.25	0.13	1.45
GR2	15/01/2009	12.3	13.7	9.0	455	91	12.5	0.6	2.32	1.65	2.6	10.6	< 5	0.1	< 5	400	73	30.0	12.0	19.3	2.17	1.33	2.85
KA1	01/02/2008	11.4	12.4	7.1	233	663	17.5	0.59	63.5	12.1	57.3	127.0	< 5	0.8	39	131	100	4.7	16.0	1.8	2.61	0.42	0.32
KA2	01/02/2008	11.8	11.5	7.3	296	578	21.3	0.69	57.7	11.7	66.1	106.0	< 5	0.6	< 5	287	50	11.0	5.4	6.3	3.45	1.04	1.59
LA1	22/01/2008	9.4	11.6	7.7	631	1094	83.0	5.1	40.2	43.2	162.0	185.0	< 5	0.9	< 5	590	1320	33.0	559.0	19.4	6.82	6.03	0.4
LA2	22/01/2008	11.0	10.7	7.3	288	118	11.8	1.05	3.56	3.49	20.6	8.54	< 5	0.4	< 5	178	460	13.0	145.0	8.5	7.26	1.99	1.2
LAS	17/02/2008	4.1	13.0	6.9	120	26	5.3	0.21	0.68	0.27	3.0	3.53	< 5	1.3	< 5	187	50	28.0	26.0	27.7	1.6	0.98	0.21
MON	01/02/2008	9.0	13.2	7.2	228	120	7.1	0.35	9.17	2.12	14.8	14.1	< 5	0.8	< 5	98	60	5.0	4.7	1.6	1.71	0.67	1.16
MUD	01/02/2008	9.4	11.4	6.9	119	601	44.3	2.12	46.3	10.1	152.0	66.3	< 5	0.2	< 5	200	150	12.0	35.0	4.6	4.47	0.92	0.23
NAD	13/02/2008	3.4	13.3	8.4	710	238	28.3	0.87	5.99	2.79	8.38	32.7	13	0.2	< 5	147	50	45.0	17.0	43.9	1.09	0.9	1.89
OM1	15/01/2009	ND	11.3	7.7	399	73	13.5	0.18	0.82	0.65	2.14	7.53	95	0.1	< 5	182	21	115.0	11.0	113.4	0.71	0.84	1.19
OM2	15/01/2009	ND	11.6	7.5	335	47	9.4	0.12	0.44	0.36	1.99	2.63	22	0.1	< 5	143	52	69.0	29.0	67.6	0.47	0.53	0.13
PHO	30/01/2008	13.0	10.6	7.5	408	184	17.4	0.27	11.0	2.7	48.9	5.7	10	0.8	< 5	38	80	7.6	206.0	4.9	1.66	1.71	1.54
RED	22/02/2008	0.9	14.0	7.8	397	198	17.8	0.52	5.47	3.38	3.58	31.4	11	0.1	30	269	130	8.8	18.0	6.1	2.1	2.27	1.56
RO1	09/02/2008	0.5	13.0	7.6	491	75	15.9	0.5	1.48	0.33	5.64	6.75	225	0.9	5	50	ND	98.0	33.0	98.0	0.7	0.34	2.35
RO2	17/02/2008	3.5	13.1	7.3	227	92	12.1	0.23	0.78	0.27	5.71	9.15	< 5	0.9	< 5	89	80	74.0	3.6	73.6	0.83	0.27	0.71
VO1	19/01/2009	7.9	12.5	7.7	496	64	6.0	0.38	4.88	1.52	1.45	3.62	< 5	0.2	< 5	279	176	11.0	15.0	4.6	2.82	0.38	0.17
VO2	19/01/2009	7.4	12.9	7.7	368	53	6.1	0.31	2.81	1.05	1.68	4.22	< 5	0.3	< 5	213	21	25.0	12.0	17.6	1.26	0.48	0.91
VO3	19/01/2009	7.7	12.5	8.0	570	72	8.4	0.45	4.4	1.65	1.51	4.07	< 5	0.1	< 5	214	31	7.0	4.3	4.3	1.3	0.84	0.36
VO4	19/01/2009	6.8	12.5	7.4	346	60	6.1	0.31	3.6	1.06	5.32	3.4	18	0.2	< 5	157	52	46.0	35.0	36.4	0.9	0.33	0.27
WHI	22/02/2008	11.0	10.7	7.6	407	184	12.2	0.65	10.6	4.51	30.6	18.0	< 5	0.8	9	141	40	4.8	10.0	1.8	1.04	0.81	0.58

Note: Oxygen saturation varied from 90–180% (median 102%); ionic strength from 0.3–13.8 (median of 1.0) mmol l^{-1}; and F^- concentrations from 0.01–0.12 (median of 0.03) mg l^{-1}. Fe and Mn concentrations determined for lakes sampled in 2009 varied within 2–45 and 0.3–8.5 µg l^{-1}, respectively. For codes, see Table I, for explanations, see Table II.

ANC = acid neutralizing capacity, ND = not determined. For other abbreviations see Table II.

Holocene transition relative sea level maximum (Nývlt, unpublished data).

Bedrock geology

The deglaciated part of the Ulu Peninsula is composed of two main geological units, namely Cretaceous back-arc basin sediments and mostly subglacial Neogene to Quaternary volcanic rocks (e.g. Olivero *et al.* 1986, Smellie *et al.* 2008, Svojtka *et al.* 2009). Four formations (Kotick Point, Whisky Bay, Hidden Lake and Santa Marta formations) of the Cretaceous James Ross Basin crop out in the study area. They are composed mostly of siltstones, sandstones and some conglomerate units (e.g. Olivero *et al.* 1986, Whitham *et al.* 2006). Back-arc, mostly subglacial, basaltic volcanic rocks of the James Ross Island Volcanic Group (JRIVG; Nelson 1966) intruded Cretaceous marine sediments since the late Miocene (Smellie *et al.* 2008, Košler *et al.* 2009). Most of the volcanic eruption took place during glacial periods below the ice cover (Smellie *et al.* 2008), which resulted in specific volcanic landforms, such as volcanic mesas (tuyas), tuff cones, dykes or subvolcanic plugs. Miocene–Pliocene glacigenic, glaciomarine and marine sediments up to >100 m thick were identified within or below the JRIVG (e.g. Nývlt *et al.* 2011).

Sampling procedures and limnological measurements

Twenty-nine representative lakes were studied during the summer season (January–February) in 2008 and 2009 (Table I, Fig. 1). We included representatives of all major lake types (according to their bedrock, origin, geomorphological position, and hydrological stability) present on the Ulu Peninsula (see below). The temperature, conductivity, concentration of dissolved oxygen and pH of the lakes were measured in the field using a YSI 600 meter. Water samples were collected from the surface layer, immediately filtered through a 200-μm polyamide sieve to remove zooplankton and coarse particles, and kept frozen until analysed at the Institute of Hydrobiology (Czech Republic). The majority of the lakes were sampled from the shore (ARG, BLA, BLU, CYA, DAN, FED, GIN, GR1–2, KA1–2, LA1–2, MUD, OM1, PHO, RED and WHI). Two lakes with persisting ice cover were sampled from their central part (NAD and RO1). A rubber boat was used for bathymetric measurements and sampling of the lakes BIB, LAS, MON, OM2, RO2 and VO1–4 (see Table I for codes). Vertical profiles of temperature, conductivity, oxygen concentration and photosynthetically active radiation (PAR) were measured in two deeper lakes under their thick ice cover (RO1 and NAD1). A quantometric sensor (400–700 nm) attached to a radiometer (PU 550, Meopta, Czech Republic) was used for PAR measurements. In two contrasting lakes (deep partially frozen RO1 and shallow LA1 without ice cover), lakewater temperature was monitored using registration thermometers (Minikin T, EMS Brno, Czech Republic) installed on the bottom of LA1 and 1 m below the ice cover of RO1. Temperature was recorded every 30 minutes from 5 January–3 February 2009.

Bathymetric mapping followed Česák & Šobr (2005). Lake shorelines were mapped with hand GPS equipment at an interval of about 5–10 m (depending on lake areas). Depth sounding was conducted using a Garmin GPSmap 178C echo sounder. The depth of shallow lakes (<0.5 m) was measured by a calibrated lath. Positions of measurements were localized by hand GPS equipment. Ground plan and depth measurements were processed using Map Info 10. Depth interpolation was processed in Surfer 8. Morphometric characteristics were calculated according to Hutchinson (1957) and bathymetric maps were created.

Water analyses

In the laboratory, samples were filtered with either membrane filters (pore size of 0.45 μm) for the determination of ions or with glass-fibre filters (pore size of 0.4 μm) for other analyses, except for samples for acid neutralizing capacity (ANC, determined by Gran titration), conductivity, and total concentrations of P, N and organic C, which were determined in unfiltered samples.

Methods used for the determination of total, dissolved, and particulate organic carbon (TOC, DOC, and PC), total, dissolved and particulate nitrogen (TN, DN, and PN), and total, dissolved, particulate, and soluble reactive phosphorus (TP, DP, PP, and SRP) are summarized in Table II. Ion concentrations (Cl^-, SO_4^{2-}, F^-, NO_3^-, NH_4^+, Ca^{2+}, Mg^{2+}, Na^+, K^+), except for NO_2^-, were determined by ion chromatography. Concentrations of NO_2^- and dissolved silica (Si) were determined spectrophotometrically (Table II). Data on ionic concentrations were used to calculate ionic strength. Concentrations of Fe and Mn were analysed by atomic absorption spectroscopy in lakes sampled in 2009. When the NO_3-N and NH_4-N concentrations were below their detection limits of 5 μg l^{-1}, half of this value was used in subsequent statistical analyses and dissolved organic nitrogen (DON) calculations (Table III). Concentrations of other constituents were always above their detection limits.

Reliability of the analytical results was checked by means of an ionic balance control approach and a comparison between measured and calculated conductivities (Kopáček *et al.* 2000). In this calculation, positive ANC values were assumed to be equal to HCO_3^- concentrations, no ANC value was ≤ 0 μmol l^{-1}. Using this approach, the differences between the sum of cations and the sum of anions ranged from -5.6 to 1.6% (with median of -0.3%) of the total ionic content.

Statistical analyses

All limnological variables except pH were log $(x+1)$ transformed and standardized prior to statistical analyses.

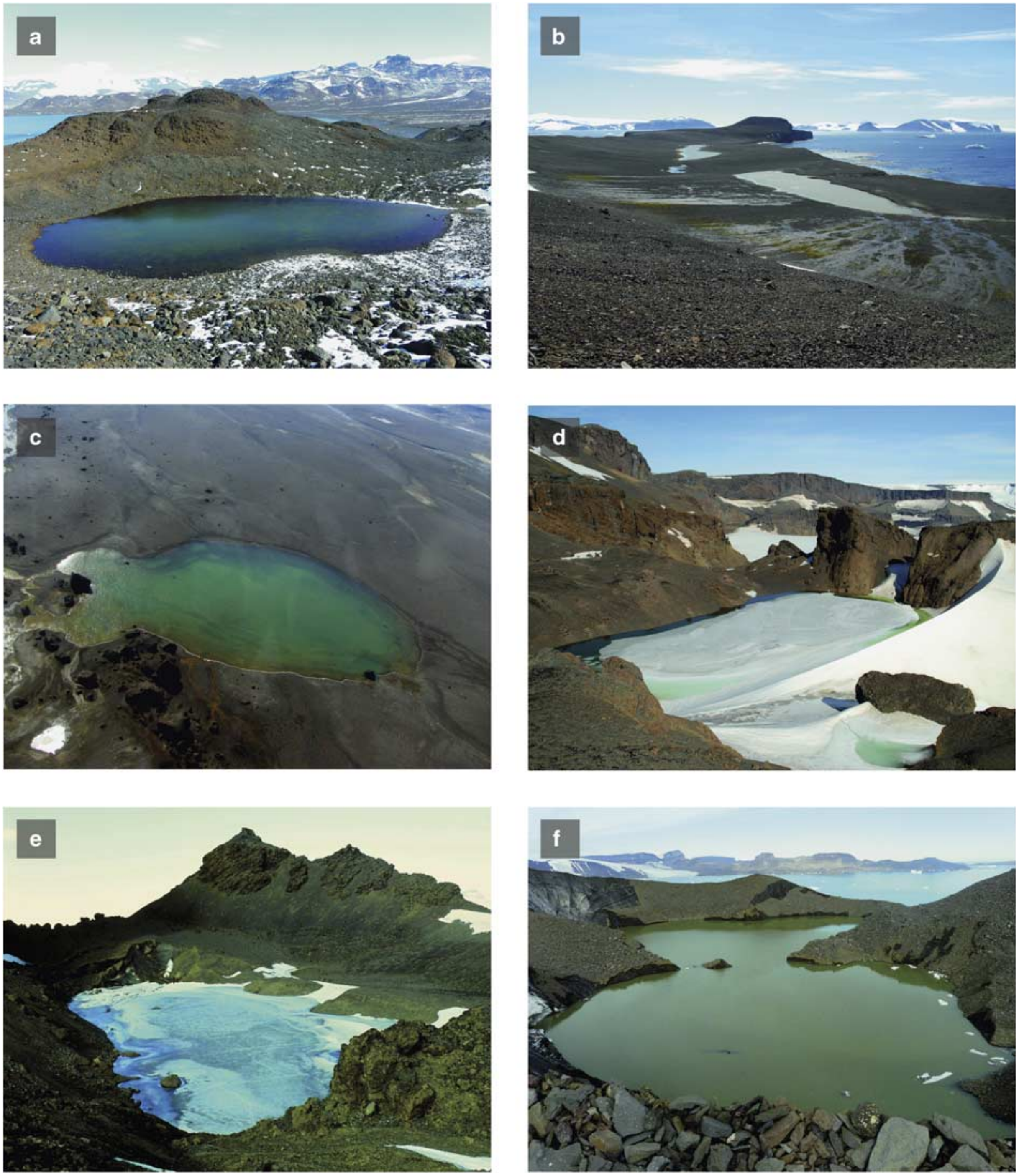

Fig. 2. Subset of lakes representing various lake types found on the Ulu Peninsula. **a**. Stable shallow lake of higher-lying levelled surfaces (type 1, RED), **b.** shallow coastal lakes (type 2, LA1–2), **c.** stable lake in old moraine (type 3, MON, picture V. Janoušek), **d.** small unstable lake in young moraine (type 4, FED), **e.** deep cirque lake (type 5, NAD), and **f.** kettle lake (type 6, OM2). For lake codes, see Table I.

First, groups of significantly correlated variables ($P < 0.05$) were identified by calculating a Spearman correlation matrix. Based on this, we selected a group of 14 representative variables, which were subsequently used in multivariate analyses. Principal component analysis (PCA) was run in Canoco 4.5 (ter Braak & Šmilauer 2002) to visualize the variability within the dataset. Since the gradient lengths in the data were short, we used redundancy analysis (RDA) to assess whether the differences in lakewater chemistry are related to lake altitude and morphology (maximal depth, lake area), lake age and bedrock characteristics. We created dummy variables for each of the bedrock types (C, V, G, M, see below) and lake ages (two age categories). In case of mixed bedrock character, a value of 0.5 was assigned to appropriate variables. Variance partitioning was applied to test the redundancy of variables or variable groups used in RDA (Borcard *et al.* 1992), which resulted in five fractions: 1) the unique effect of lake morphology, 2) the unique effect of lake age, 3) the unique effect of bedrock type, 4) overlap between 1–3, and 5) unexplained variation.

Results

Bedrock type

Lakes at the northern deglaciated part of the Ulu Peninsula occurred on four main bedrock types (Table I).

The first group of lakes (DAN, KA1, KA2, MUD and partly MON, PHO) lie on Cretaceous marine sediments (bedrock C). All of these lakes are situated in the area where the Santa Marta Formation crops out, hence their bedrock is rather calcareous and is composed predominantly of sandstone and siltstone units, from which corresponding grain-size fractions originate.

Higher-lying lakes located on levelled surfaces lie predominantly on volcanic mesas or lowered volcanic surfaces. Therefore, their bedrock is composed of Neogene basaltic volcanic rocks comprising mainly sub-aerial cap basalts, hyaloclastite breccias and tuffs (bedrock V).

The third group of lakes (LA1–2 and partly MON, PHO) lie in the area of glacial sediment drapes, which are composed dominantly of local Neogene basaltic volcanic rocks and Cretaceous marine sediments (partly calcareous) with some admixture of erratic material (mostly metasediments and granitoids) derived from the Antarctic Peninsula (bedrock G).

The last and most common group of lakes lies in recent glacial (morainic) sediments connected with glaciers (bedrock M). As these glaciers originate mostly from volcanic mesa slopes or surfaces, they mostly carry local volcanic rocks. However, some admixture of Cretaceous marine sediments cannot be excluded, as Cretaceous material has been found, for example, in the frontal moraine of Whisky Glacier.

Lake types

According to their origin, geomorphological position and hydrological stability, six lake types can be distinguished on the Ulu Peninsula (Table I):

1) Stable shallow lakes on higher-lying levelled surfaces (BLA, CYA, GR1–2, RED, VO1–4, WHI, Fig. 2a). These lakes are among the oldest in the studied region. The last deglaciation of these glacially-levelled volcanic surfaces took place during the early Holocene and the lakes must have originated after that. Therefore, the lakes are regarded as permanent and old to very old, with a persistence of hundreds to thousands of years. Their winter ice cover melts at the beginning of summer. They are situated mostly in the south-eastern part of the study area not far from the coastline at middle to higher altitudes (40–185 m a.s.l.). The lakes are mostly small and shallow with a maximum depth of typically < 1.5 m. Lakes VO1–4 lie farther from the coast at altitudes 221–235 m a.s.l. They are the largest and deepest (up to 3.7 m) within this group.
2) Shallow coastal lakes (LA1–2, MUD, Fig. 2b). These lakes developed mostly in the early to mid Holocene, following relative sea level fall and/or glacier retreat in the coastal areas. LA1–2 and MUD are of oblong form, very shallow (maximum depth is only 0.3 m) and lie in the proximity of the sea at very low altitudes. High aeolian input of silty–sandy material originating mostly from Cretaceous sediment affects depositional rates, their bottoms are therefore composed of a thick (up to > 2 m) layer of sediments. High sediment deposition and irregular water supply mostly from thawing snow patches limit their stability and we cannot exclude desiccation events during the history of these shallow lakes. This was confirmed in February 2012, when LA1 was found dry (M. Barták, personal communication 2012). This lake group was most probably formed during the mid-Holocene times. These lakes are very old (they are present for thousands of years) and semi-permanent, as seasonal drying cannot be excluded.
3) Stable lakes in old moraines (DAN, KA1–2, MON, PHO, Fig. 2c). Advancing local glaciers accumulated large morainal ridges during the Holocene neoglacial period, degradation of which created numerous lakes. Only the largest and most stable have lasted until the present. Hence these lakes are permanent and very old, with their persistence in the order of thousands of years. They are located in the western part of the study area at low to mid-altitudes. They have a very similar slightly oblong form, and their surface area varies from 1500–158 100 m^2. These lakes are very shallow (maximum depth 0.5 m), with the exception of the higher situated MON (77 m a.s.l.), which is up to 2.2 m deep.
4) Small unstable lakes in young moraines (BIB, FED, Fig. 2d). Young moraines in front of retreating local glaciers host small lakes with mostly stony bottoms, which are usually ephemeral. They are young and originated from the last retreat of local glaciers. Their maximum expected age could be approximately a century or only some decades. They are ephemeral, as they are mostly ice-dammed marginal lakes and further glacier thawing may induce their complete discharge. Their surface and catchment areas are amongst the smallest of the studied lakes. They have a rather elongate form with quite high maximum depths.

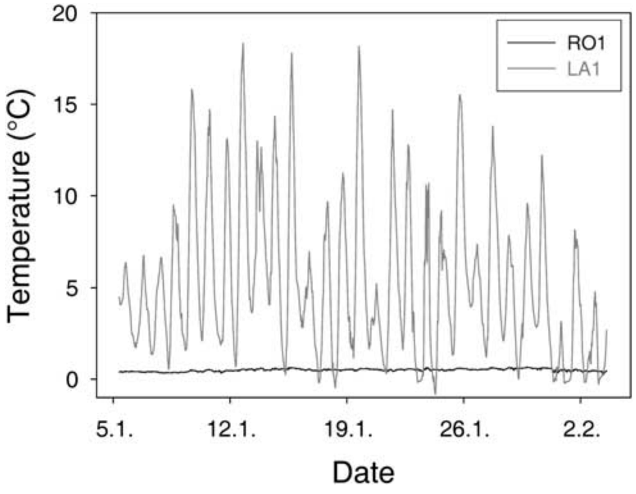

Fig. 3. Lakewater temperature recorded by registration thermometers at 30 min intervals in a cirque (RO1) and a shallow coastal lake (LA1) from 5 January–3 February 2009.

5) Deep cirque lakes (NAD, RO1, Fig. 2e). Deep glacial cirques occur on the lee sides of some volcanic mesas, where accumulation of drifting snow allowed the formation of cirque glaciers. Numerous cirque lakes have evolved due to the recent decay of local glaciers on James Ross Island. Their key feature is the presence of extensive ice cover, which persists at least partly during summer. These lakes are stable in the order of tens of years, however, further thawing due to increasing temperatures will induce their decay. We may therefore assign them as being less-stable. They are young and, similar to the unstable lakes in young moraines, probably originated during the last retreat of local glaciers. RO1 and NAD have morphometric parameters typical for cirque lakes, they have large water volumes and very high maximum and relative depths.

6) Kettle lakes (ARG, BLU, GIN, LAS, OM1–2, RO2, Fig. 2f). The youngest and least stable lakes have evolved in debris covered glacier systems by ice degradation in kettle-holes, which have subsequently filled with water. These lakes are the most abundant lake type on James Ross Island. They might persist for years or a few decades only. Therefore, we assign them as being very young and ephemeral. Their surface area varies from 1500–16 500 m^2. The maximum and relative depths are also very high and temporarily variable. Depth soundings were done only on three kettle lakes, so it is not possible to provide a detailed comparison with the other lake types.

Detailed morphometric parameters are presented in Table I. Bathymetric maps of 23 lakes are given as Figs S1–S23, which will be found at http://dx.doi.org/10.1017/S0954102012000934.

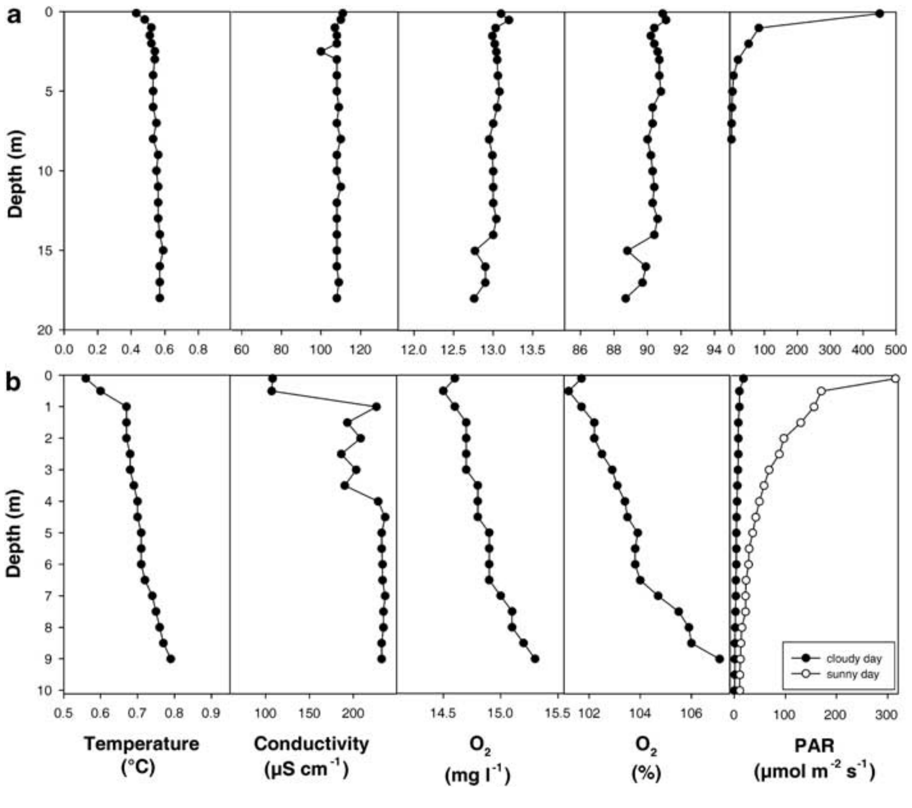

Fig. 4. Vertical profiles of the main physical and chemical parameters in two cirque lakes. **a.** RO1 (9 February 2008), and **b.** NAD (13 February 2008). Photosynthetically active radiation (PAR) in NAD was also measured on 14 February 2008 (sunny day).

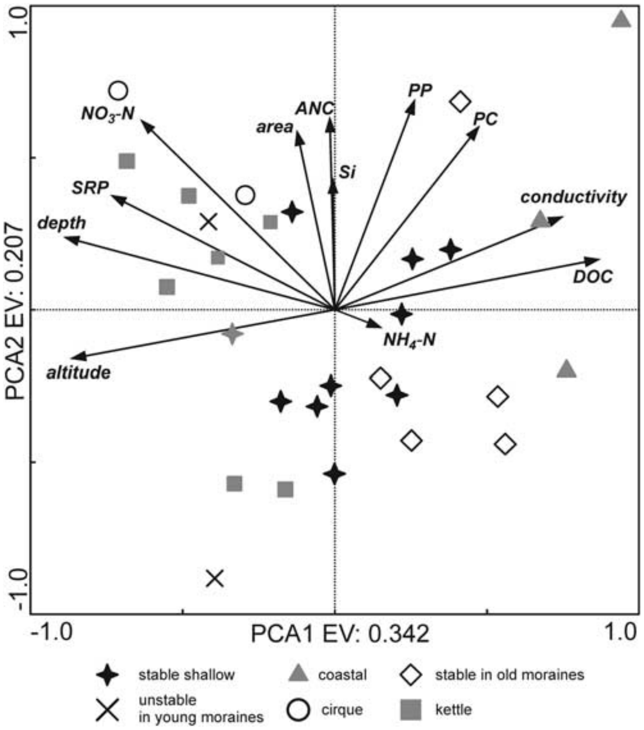

Fig. 5. Principal component analysis (PCA) showing the correlation of the main limnological characteristics of the lakes. The position of individual lakes within the diagram is indicated, together with the information about lake type. For abbreviations, see Table II.

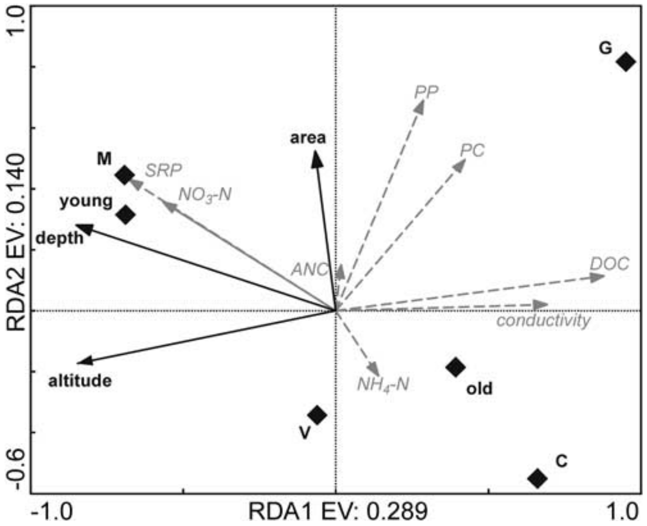

Fig. 6. The influence of bedrock, lake age, and lake altitude and morphometry on water chemistry (redundancy analysis). For details, see text. Old = lake types 1, 2, 3; young = lake types 4, 5, 6. C = Late Cretaceous marine sediments, G = Miocene–Holocene glacial sediments composed mostly of local volcanic rocks and marine Cretaceous sediments, M = recent glacial sediments, and V = Neogene volcanic rocks. For more abbreviations, see Table II.

Physical characteristics

The lakes were ice-free in January–February of 2008 and 2009, with the exception of FED, NAD and RO1–2. Ice break-up of RO2 was observed in mid-February 2008 and this kettle lake was found dry in 2009.

NAD and RO1 are deep cirque lakes and were covered by ice, which was up to 2 m thick and had a characteristic candle-ice structure (up to 30 cm long) at the time of sampling. With the progressing summer season, these two lakes started to melt at the margins and approximately half of their area became ice-free by February 2008. In 2009, the melting progressed more quickly in January, but was interrupted by rapid cooling in February. FED is situated in a young moraine at the highest altitude of all the lakes (Table I) and its whole surface was frozen at the end of January 2009. However, water was present under a thin ice layer close to the shoreline.

The thermal regime of the lakes was mainly driven by their geomorphological and hydrological position. Important diurnal temperature fluctuations were observed in shallow lakes. In LA1, water temperature ranged from a maximum of 18.2°C to a minimum of -0.8°C (period from 5 January–3 February 2009). Mean (± standard deviation) water temperature was 5.3 ± 4.1°C and the maximum diurnal fluctuation (17.1°C) was observed on 12 January 2009. Subzero episodes were more frequent towards the end of the season. As expected, very stable temperature conditions occurred in the deep frozen lakes: the temperature of RO1 (cirque lake) 1 m below the ice was 0.5 ± 0.1°C during the period of measurement (Fig. 3). In 2009, over-winter temperature logging in the central part of LA1 showed a rapid freezing of the lake at the end of the summer and subzero temperatures at the sediment surface during the entire winter.

The oxygen concentration was close to the saturation point in the majority of the lakes (Table III). High oxygen oversaturation coincided with weather conditions being favourable for photosynthesis at the time of sampling.

Except PAR, the vertical profiles of the basic physical and chemical parameters measured were almost stable in RO1 down to the depth of 20 m. Photosynthetically active radiation was attenuated at a depth of 8 m, which corresponded to a vertical extinction coefficient of 1.1 m^{-1} (Fig. 4a). In NAD, only a small amount of variation was observed with increases in temperature, conductivity and oxygen concentration towards the bottom. Photosynthetically active radiation profiles were measured on two contrasting days (sunny and cloudy) with *c.* 2% of the surface PAR reaching the lake bottom (extinction coefficient 0.4 m^{-1}, Fig. 4b). The ice cover of this lake was retreating in the littoral zone at the time of sampling.

Water chemistry

Lakewater pH was circum neutral to slightly alkaline (6.8–9.5). The other chemical parameters were highly variable (Table III).

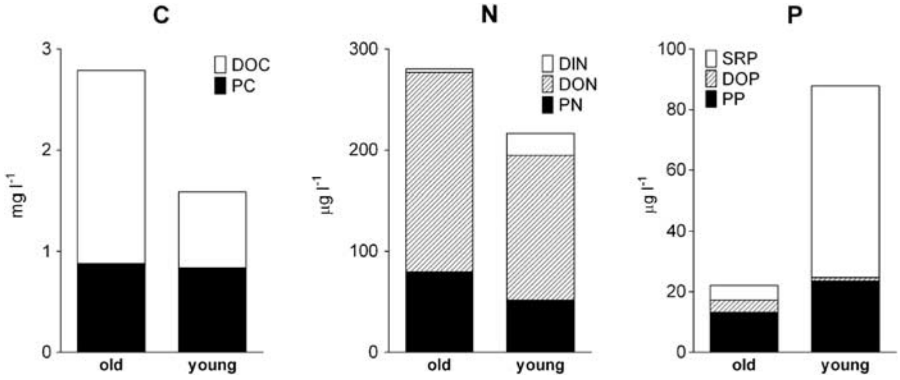

Fig. 7. Concentrations of carbon (C), nitrogen (N) and phosphorus (P) fractions in old and young lakes (medians). The differences were statistically significant for dissolved organic carbon (DOC, $P = 0.0002$), dissolved inorganic nitrogen (DIN, $P = 0.03$), dissolved reactive phosphorus (SRP, $P < 0.0001$) and dissolved organic phosphorus (DOP, $P = 0.003$). For more abbreviations, see Table II.

Conductivities were in the range 25–1094 µS cm^{-1} (median 91 µS cm^{-1}). Due to the strong correlation between conductivity and the concentrations of Ca^{2+}, K^{+}, Mg^{2+}, SO_4^{2-} and Cl^{-} (all $P < 0.0001$), only conductivity was used in the subsequent multivariate analyses. The PCA of all lakes revealed that conductivity and DOC concentration were positively correlated and depth, altitude and SRP were negatively correlated with the first PCA axis. Hence, these variables govern the main limnological diversity in the region. The second PCA axis was most correlated with ANC and lake surface area. High conductivity and DOC values were characteristic for shallow coastal lakes (type 2). Soluble reactive phosphorus and NO_3-N concentrations were high in the deep kettle (type 6) and cirque lakes (type 5) at higher altitudes. Stable lakes (types 1 and 3) showed a rather diverse lakewater chemistry. Overall, there was a gradual transition of lake types along the first axis (Fig. 5, Table III).

The significant relationship between lake type and lakewater chemistry (conductivity, ANC and concentrations of DOC, PC, DON, PN, NH_4-N, NO_3-N, PP and SRP) was confirmed by RDA (not shown). To identify the characteristics explaining the greatest amount of variation in lakewater chemistry, we performed RDA and subsequent variance partitioning with the following variables or variable groups: 1) bedrock: C, G, V, M (see Bedrock type and Table I), 2) lake age (see Lake types), and 3) lake altitude and morphometry (maximum depth, lake area). All the canonical axes together explained 60.4% of the total variability in lakewater chemistry. The unique contributions of the individual variables were as follows: bedrock (14.2%), lake age (9.8%) and lake altitude and morphometry (8.2%). The proportion of the variability explained jointly by these characteristics without the possibility of separating their effects was a further 28.2%. The redundancy of the variables in explaining lakewater chemistry was thus quite high, because they were highly intercorrelated (Fig. 6). The proportion of unexplained variation was 39.6%.

To identify the sources of the major ions in the lakewater, we compared their ratios to those of seawater. The highest concentrations of Na^{+}, K^{+}, Ca^{2+}, Mg^{2+}, SO_4^{2-} and Cl^{-} were recorded in coastal lakes (type 2) close to the sea shore with medians of 44.3, 2.1, 40.2, 10.1, 152.4 and 66.4 mg l^{-1}, respectively. Other lake types were characterized by significantly lower concentrations of these ions (Table III).

All the catchments were the source of HCO_3^{-} and almost all were also the source of Ca^{2+}. Concentrations of Ca^{2+} were generally low with a median of 4.4 mg l^{-1}. However, some lakes exhibited one order of magnitude higher Ca^{2+} concentrations (e.g. 58–64 mg l^{-1} in KA1 and KA2). Evidence for additional sources from the catchment has also been found for Na^{+}, K^{+}, Mg^{2+}, SO_4^{2-}, Cl^{-} and NO_3-N. Furthermore, the ionic ratios suggested internal alkalinity generation in several lakes with high NO_3-N concentrations (OM1, OM2 and RO1, Table III).

We observed higher concentrations of DOC in older lakes (with a median of 1.91 mg l^{-1}, in comparison to 0.70 mg l^{-1} in young lakes). This was also the cause of their difference in TOC. The same pattern in relation to lake age was observed for dissolved organic phosphorus (DOP) with medians of 4.1 µg l^{-1} (old lakes) and 1.1 µg l^{-1} (young lakes, Fig. 7).

The lakes also exhibited a significant difference in dissolved inorganic nitrogen (DIN) and SRP concentrations, with elevated values in young lakes at higher altitudes (Fig. 7). The concentrations reached up to 220 µg l^{-1} NO_3-N (in RO1) and 113 µg l^{-1} SRP (in OM1).

Particulate nutrient concentrations (PC, PN and PP) were very variable, with highest values in the coastal lake LA1 (Table III). In contrast to dissolved nutrients, there were no significant differences in PC, PN, PP and their ratios between the two lake age categories.

Discussion

Stable shallow lakes on higher-lying levelled surfaces originated after the deglaciation of volcanic mesas. Johnson *et al.* (2011) showed that higher-lying areas of the Ulu Peninsula were ice-free some 6.5–8 ka ago. However, later appearance of these lakes is also possible, as we have no exact dates from their sediments. Shallow coastal lakes formed after *c.* 7000 yr BP following relative sea level fall (Hjort *et al.* 1997). The coastal lake at lower altitude

(MUD) was formed probably sometime after 3000 yr BP according to regional relative sea level curves (Roberts *et al*. 2011). Small unstable lakes in young moraines originated from glacial retreat since the last advance of local glaciers (Carrivick *et al.* in press). Although we have no exact timing of this advance, it could be correlated with the Little Ice Age and therefore the maximum expected age of these lakes could be approximately a century or rather some decades. The same is true for the deep cirque lakes, which evolved due to recent decay of local glaciers on James Ross Island (e.g. Carrivick *et al.* in press). Kettle lakes are, on the contrary, very ephemeral, as their outbursts are quite common. One of these events was recently described by Sone *et al*. (2007).

In summary, the oldest lakes from our dataset are shallow coastal lakes (type 2), together with stable lakes in old moraines (type 3) and partly with stable shallow lakes of higher-lying levelled surfaces (type 1). Young lakes are represented by deep cirque lakes (type 5), small unstable lakes in young moraines (type 4), and the youngest kettle lakes (type 6). The lakes of the Ulu Peninsula are thus relatively young in comparison with other regions in Antarctica (Vincent & Laybourn-Parry 2008). Based on their geomorphological and hydrological stability, the most stable are shallow lakes of higher-lying levelled surfaces (type 1) and lakes in old moraines (type 3), followed by semi-stable shallow coastal lakes (type 2), less-stable deep cirque lakes (type 5), and small unstable lakes in young moraines (type 4). Kettle lakes (type 6) are very ephemeral.

The high diversity of lake types found on the relatively small area of the Ulu Peninsula underlies the variable physical and chemical characteristics of the lakes. Due to the harsher climatic conditions on James Ross Island, the timing of ice break-up is probably slightly delayed in comparison with lakes on the western side of the Antarctic Peninsula (Toro *et al*. 2007). Some lakes at higher altitudes may even remain permanently ice-covered. However, comparison of the two sampling years showed that the ice cover status of the lakes is obviously very variable in climatically different years. Except for LA1, we have no direct evidence that no liquid water occurred under the ice cover of other shallow lakes over winter. Freezing dynamics has been demonstrated as a very important factor structuring the chemistry and biological communities of Antarctic shallow lakes (Hawes *et al*. 2011) and is closely related to lake depth (Sabbe *et al*. 2004). At the time of sampling, light reached the bottom in most of the lakes with the exception of the deep cirque lake RO1 and probably several kettle lakes (e.g. ARG, OM1–2, vertical profiles not measured), which were very turbid. High turbidity also reduced light penetration in coastal lakes (type 2), which receive a high input of fine material originating from Cretaceous sediment.

The lowest pH, ANC and conductivity values, which were found in BIB, were probably associated with the intensive ice cover thawing at the time of sampling, which resulted in a decrease in ionic composition. Ice cover dynamics can apparently affect the chemical composition of lakewater, as was demonstrated by Verleyen *et al*. (2012) for a large set of Antarctic lakes. On the other hand, pH values around 9 were recorded in lakes with high oxygen concentrations, suggesting the influence of photosynthesis on pH (see above).

A strong marine influence on lakewater chemistry, decreasing with lake altitude, was confirmed. Distance to the coastline was already identified as one of the important factors driving water chemistry of glacial lakes in East Antarctica (Borghini *et al*. 2008, Verleyen *et al*. 2012). The highest conductivity was recorded in the shallow coastal lake LA1 (1094 μS cm^{-1}), which is strongly influenced by sea spray due to its geomorphological position (Fig. 1). In contrast to the neighbouring LA2, with one order of magnitude lower conductivity, it lacks the constant supply of meltwater from the permanent snowfields above the lake (Fig 2b). Brackish and saline lakes, which are common elsewhere in Antarctica (Vincent & Laybourn-Parry 2008), are absent on the Ulu peninsula, because the lakes are of glacial origin and relatively young (Verleyen *et al*. 2012).

The effect of bedrock on lakewater chemistry was also apparent especially in the case of the lakes in the Brandy Bay area (Fig. 1). These lakes belong mostly to type 3 (stable lakes in old moraines), and their chemistry is influenced by a strong enrichment from their Cretaceous bedrock. In fact, bedrock diversity was identified by variance partitioning as the most important factor driving lakewater chemistry on the Ulu Peninsula. A significant contribution of rock weathering to lakewater chemistry has been previously reported from Antarctica (e.g. Borghini & Bargagli 2004).

Furthermore, we observed significant differences in nutrient chemistry between old (lake types 1, 2, 3) and young lakes (lake types 4, 5, 6; Fig. 7). The positive relationship between DOC concentrations and lake age was reported by various authors (e.g. Engstrom *et al*. 2000). The highest DOC values were typical for very shallow coastal lakes (type 2), which were characterized by prominent benthic microbial mats. On the other hand, the low DOC concentrations in young lakes are comparable with those observed in the most oligotrophic Antarctic lakes (Vincent & Laybourn-Parry 2008). DOP concentrations were also significantly lower in young lakes with values similar to the extreme meltwater habitats of the Darwin Glacier (Victoria Land, Webster-Brown *et al*. 2010), which probably reflects their lower productivity in comparison with old lakes.

High concentrations of NO_3-N in several young lakes cannot be solely explained by atmospheric input (e.g. Aristarain *et al*. 1982). Overall, high nitrate concentrations in lakewater are not exceptional in Antarctica. Important sources of N for Antarctic lakes and ponds are bird rookeries and marine mammals (Toro *et al*. 2007, Borghini *et al*. 2008).

However, these factors can be excluded on the Ulu Peninsula, since animal activity is very limited and virtually absent at higher altitudes, where lakes with high DIN concentration occur. We believe that neither nitrogen fixing cyanobacteria were the source of N, because microbial mats were poorly developed in the littoral zone of the lakes with the highest NO_3-N concentrations. According to Priscu (1995), the high levels of nutrients recorded in the deep waters of the Dry Valley lakes represent a legacy related to the origin of the lakes, but this could also hardly be the case of the James Ross Island lakes. Consistently high nitrate concentrations ($> 100\ \mu g\ N\ l^{-1}$) are characteristic for inland waters of the Ross Ice Shelf region (Vincent & Howard-Williams 1994, Webster-Brown *et al.* 2010). The nitrate enrichment in this region was attributed to concentration mechanisms, such as freezing and evaporation, and there was a close positive correlation between NO_3-N concentrations and conductivity. In addition, the chloride to nitrate ratio was within the range reported for Antarctic snow, indicating that nitrate was probably derived from snowmelt (Vincent & Howard-Williams 1994). In the case of extreme values (up to $13\ g\ N\ l^{-1}$), nitrate-bearing salts were the source of N (Webster-Brown *et al.* 2010). In contrast to Ross Ice Shelf waters, there was no correlation between NO_3-N concentrations and conductivity in our dataset (Fig. 5), indicating a different N origin. Recently, Morford *et al.* (2011) suggested the possible role of bedrock as an alternative N source. Unfortunately, we have no direct information about the N content in rocks prevailing in the young moraines which form the catchments of young lakes on James Ross Island. Young lakes were also characterized by significantly higher concentrations of SRP indicating a P source in their catchments (Fig. 7). In the lakes of the Byers Peninsula (Livingston Island), SRP concentrations were low. Values comparable to the young lakes of the Ulu Peninsula were recorded only in a hypereutrophic lake, which was influenced by marine mammals (Toro *et al.* 2007).

There is evidence that there are still unidentified but important N and P sources in the catchments of several young lakes on James Ross Island. Moreover, the differences in NO_3-N and SRP concentrations between old and young lakes can also be influenced by the rate of primary production. However, we have only qualitative information about autotrophic biomass, which was significantly lower in young lakes. To analyse these differences in more detail, data on nutrient input to the lakes together with their photosynthetic rates would be necessary. Increasing NO_3-N concentrations with decreasing lake productivity were already observed in several Antarctic regions (Healy *et al.* 2006, Borghini *et al.* 2008).

For many lakes on James Ross Island, the molar PC:PP and PN:PP ratios of the epilimnetic seston are lower than: 1) the C:P and N:P ratios of marine plankton which have been inferred to be an indication of the nutrient-sufficient status of plankton (106 and 16, respectively; Redfield 1958), and 2) the C:P and N:P ratios of plankton in temperate lakes with P limited growth (306 and 24, respectively; Hecky *et al.* 1993), suggesting that the lakes could be N-limited. In lakes with high NO_3-N and SRP concentrations (types 4–6), the PN:PP ratio remained relatively low, but nutrients were unlikely to be limiting. Physical factors, such as low light and temperature, are important constraints on production in many Antarctic lakes (Vincent & Laybourn-Parry 2008). However, NO_3-N concentrations were usually depleted in shallow lakes with important benthic mats (types 1–3) (Table III). It was previously shown that nutrient limitation can also be significant in Antarctic lakes. Based on experimental enrichments, both N and P limitation were reported from the Dry Valley lakes (Priscu 1995). Recently, Barrett *et al.* (2007) demonstrated the great influence of landscape age on the C:N:P stoichiometry in Taylor Valley with lower N:P ratios in streams on younger surfaces. Thus, the relative excess of P in the James Ross Island lakes could reflect their generally younger age connected with harsher climatic conditions in comparison with other lake districts in the Antarctic Peninsula region (e.g. Byers Peninsula on Livingston Island, Toro *et al.* 2007). Based on our data, however, it is not possible to determine exactly the character of limitation in lakes of the Ulu Peninsula.

Conclusions

Six lake types have been defined for the northern deglaciated part of the Ulu Peninsula, James Ross Island. These are: 1) Stable shallow lakes of higher-lying levelled surfaces, 2) shallow coastal lakes, 3) stable lakes in old moraines, 4) small unstable lakes in young moraines, 5) deep cirque lakes, and 6) kettle lakes. Lakes basically differ in their origin and history, which influences their morphometry, hydrological stability, and physical and chemical characteristics. The diversity of lakes is further related to the differences in bedrock composition. Therefore, the lakes on James Ross Island represent a very valuable set of lacustrine habitats in the transitional zone between maritime and continental Antarctica.

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Supplementary material

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References

Aristarain, A.J., Delmas, R.J. & Briat, M. 1982. Snow chemistry on James Ross Island (Antarctic Peninsula). *Journal of Geophysical Research*, **87**, 11 004–11 012.

Aristarain, A.J., Pinglot, J.F. & Pourchet, M. 1987. Accumulation and temperature measurements on the James Ross Island, Antarctic Peninsula, Antarctica. *Journal of Glaciology*, **33**, 357–362.

Barrett, J.E., Virginia, R.A., Lyons, W.B., McKnight, D.M., Priscu, J.C., Doran, P.T., Fountain, A.G., Wall, D.H. & Moorhead, D.L. 2007. Biogeochemical stoichiometry of Antarctic Dry Valley ecosystems. *Journal of Geophysical Research*, **112**, 1–12.

Bendschneider, K. & Robinson, R.J. 1952. A new spectrophotometric method for the determination of nitrite in sea water. *Journal of Marine Research*, **11**, 87–96.

Björck, S., Olsson, S., Ellis-Evans, C., Håkansson, H., Humlum, O. & de Lirio, J.M. 1996. Late Holocene palaeoclimatic records from lake sediments on James Ross Island, Antarctica. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **121**, 195–220.

Borcard, D., Legendre, P. & Drapeau, P. 1992. Partialling out the spatial component of ecological variation. *Ecology*, **73**, 1045–1055.

Borghini, F. & Bargagli, R. 2004. Changes of major ion concentrations in melting snow and terrestrial waters from northern Victoria Land, Antarctica. *Antarctic Science*, **16**, 107–115.

Borghini, F., Colacevich, A., Caruso, T. & Bargagli, R. 2008. Temporal variations in the water chemistry of northern Victoria Land lakes (Antarctica). *Aquatic Science*, **70**, 134–141.

Carrivick, J.L., Davies, B.J., Glasser, N.F., Nývlt, D. & Hambrey, M.J. In press. Late Holocene changes in character and behaviour of land-terminating glaciers on James Ross Island, Antarctica. *Journal of Glaciology*.

Česák, J. & Šobr, M. 2005. Methods of bathymetric mapping of Czech lakes. *Geografie*, **110**, 141–151.

CGS (Czech Geological Survey). 2009. *James Ross Island - northern part*. Topographic map, 1:25 000. Prague: Czech Geological Survey.

Davies, B.J., Glasser, N.F., Carrivick, J.L., Hambrey, M.J., Smellie, J.L. & Nývlt, D. In press. Landscape evolution and ice-sheet behaviour in a semi-arid polar environment: James Ross Island, NE Antarctic Peninsula. *Special Publication, Geological Society of London*.

Engel, Z., Nývlt, D. & Láska, K. 2012. Ice thickness, areal and volumetric changes of Davies Dome and Whisky Glacier in 1979–2006 (James Ross Island, Antarctic Peninsula). *Journal of Glaciology*, **58**, 904–914.

Engstrom, D.R., Fritz, S.C., Almendinger, J.E. & Juggins, S. 2000. Chemical and biological trends during lake evolution in recently deglaciated terrain. *Nature*, **408**, 161–166.

Fukui, K., Sone, T., Strelin, J.A., Torielli, C.A., Mori, J. & Fujii, Y. 2008. Dynamics and GPR stratigraphy of a polar rock glacier on James Ross Island, Antarctic Peninsula. *Journal of Glaciology*, **54**, 445–451.

Golterman, H.L. & Clymo, R.S. 1969. *Methods for chemical analysis of fresh waters*. Oxford: Blackwell, 172 pp.

Hawes, I., Safi, I., Sorrel, B., Webster-Brown, J.G., Brown, K.L. & Arscott, D. 2011. Summer–winter transitions in Antarctic ponds I: The physical environment. *Antarctic Science*, **23**, 235–242.

Healy, M., Webster-Brown, J.G., Brown, K.L. & Lane, V. 2006. Chemistry and stratification of Antarctic meltwater ponds II: Inland ponds in the McMurdo Dry Valleys, Victoria Land. *Antarctic Science*, **18**, 525–533.

Hecky, R.E., Campbell, P. & Hendzel, L.L. 1993. The stoichiometry of carbon, nitrogen, and phosphorus in particulate matter of lakes and oceans. *Limnology and Oceanography*, **38**, 709–724.

Hjort, C., Ingólfsson, Ó., Möller, P. & Lirio, J.M. 1997. Holocene glacial history and sealevel changes on James Ross Island, Antarctic Peninsula. *Journal of Quaternary Science*, **12**, 259–273.

Hutchinson, E.G. 1957. *A treatise on limnology.* Vol. I. *Geography, physics and chemistry*. New York: John Wiley & Sons, 1015 pp.

Johnson, J.S., Bentley, M.J., Roberts, S.J., Binnie, S.A. & Freeman, S.P.H.T. 2011. Holocene deglacial history of the northeast Antarctic Peninsula - A review and new chronological constraints. *Quaternary Science Reviews*, **30**, 3791–3802.

Komárek, J. & Elster, J. 2008. Ecological background of cyanobacterial assemblages of the northern part of James Ross Island, Antarctica. *Polish Polar Research*, **29**, 17–32.

Kopáček, J. & Hejzlar, J. 1993. Semi-micro determination of total phosphorus in fresh waters with perchloric acid digestion. *International Journal of Environmental Analytical Chemistry*, **53**, 173–183.

Kopáček, J., Hejzlar, J. & Mosello, R. 2000. Estimation of organic acid anion concentrations and evaluation of charge balance in atmospherically acidified colored waters. *Water Research*, **34**, 3598–3606.

Košler, J., Magna, T., Mlčoch, B., Mixa, P., Nývlt, D. & Holub, F.V. 2009. Combined Sr, Nd, Pb and Li isotope geochemistry of alkaline lavas from northern James Ross Island (Antarctic Peninsula) and implications for back-arc magma formation. *Chemical Geology*, **258**, 207–218.

Morford, S.L., Houlton, B.Z. & Dahlgren, R.A. 2011. Increased forest ecosystem carbon and nitrogen storage from nitrogen rich bedrock. *Nature*, **477**, 78–81.

Murphy, J. & Riley, J.P. 1962. A modified single-solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta*, **27**, 31–36.

Nelson, P.H.H. 1966. The James Ross Island Volcanic Group of north-east Graham Land. *British Antarctic Survey Scientific Reports*, **54**, 62 pp.

Nývlt, D., Košler, J., Mlčoch, B., Mixa, P., Lisá, L., Bubík, M. & Hendriks, B.W.H. 2011. The Mendel Formation: evidence for Late Miocene climatic cyclicity at the northern tip of the Antarctic Peninsula. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **299**, 363–384.

Olivero, E.B., Scasso, R.A. & Rinaldi, C.A. 1986. Revision of the Marambio Group, James Ross Island, Antarctica. *Instituto Antartico Argentino, Contribución*, **331**, 1–28.

Priscu, J.C. 1995. Phytoplankton nutrient deficiency in lakes of the McMurdo Dry Valleys, Antarctica. *Freshwater Biology*, **34**, 215–227.

Quayle, W.C., Peck, L.S., Peat, H., Ellis-Evans, J.C. & Harrigan, P.R. 2002. Extreme responses to climate change in Antarctic lakes. *Science*, **295**, 645.

Redfield, A.C. 1958. The biological control of chemical factors in the environment. *American Scientist*, **46**, 205–221.

Roberts, S.J., Hodgson, D.A., Sterken, M., Whitehouse, P.L., Verleyen, E., Vyverman, W., Sabbe, K., Balbo, A., Bentley, M.J. & Moreton, S.G. 2011. Geological constraints on glacio-isostatic adjustment models of relative sea level change during deglaciation of Prince Gustav Channel, Antarctic Peninsula. *Quaternary Science Reviews*, **30**, 3603–3617.

Sabbe, K., Hodgson, D.A., Verleyen, E., Taton, A., Wilmotte, A., Vanhoutte, K. & Vyverman, W. 2004. Salinity, depth and the structure and composition of microbial mats in continental Antarctic lakes. *Freshwater Biology*, **49**, 296–319.

Siegert, M.J., Carter, S., Tabacco, I., Popov, S. & Blankenship, D. 2005. A revised inventory of Antarctic subglacial lakes. *Antarctic Science*, **17**, 453–460.

Smellie, J.L., Johnson, J.S., McIntosh, W.C., Esser, R., Gudmundsson, M.T., Hambrey, M.J. & van Wyk de Vries, B. 2008. Six million years of glacial history recorded in volcanic lithofacies of the James Ross Island Volcanic Group, Antarctic Peninsula. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **260**, 122–148.

Sone, T., Fukui, K., Strelin, J.A., Torielli, C.A. & Mori, J. 2007. Glacier lake outburst flood on James Ross Island, Antarctic Peninsula region. *Polish Polar Research*, **28**, 3–12.

Sterken, M., Roberts, S.J., Hodgson, D.A., Vyverman, W., Balbo, A.L., Sabbe, K., Moreton, S.G. & Verleyen, E. 2012. Holocene glacial and climate history of Prince Gustav Channel, northeastern Antarctic Peninsula. *Quaternary Science Reviews*, **31**, 93–111.

Svojtka, M., Nývlt, D., Murakami, M., Vávrová, J., Filip, J. & Mixa, P. 2009. Provenance and post-depositional low-temperature evolution of the James Ross Basin sedimentary rocks (Antarctic Peninsula) based on fission track analysis. *Antarctic Science*, **21**, 593–607.

ter Braak, C.J.F. & Šmilauer, P. 2002. *CANOCO reference manual and user's guide to Canoco for Windows: software for Canonical Community Ordination* (Version 4.5). Ithaca, NY: Microcomputer Power, 500 pp.

Toro, M., Camacho, A., Rochera, C., Roco, E., Banon, M., Fernandez-Valiente, E., Marco, E., Justel, A., Avendano, M.C., Ariosa, Y., Vincent, W.F. & Quesada, A. 2007. Limnological characteristics of the freshwater ecosystems of Byers Peninsula, Livingston Island, in Maritime Antarctica. *Polar Biology*, **30**, 635–649.

Vaughan, D.G., Marshall, G.J., Connolley, W.M., Parkinson, C., Mulvaney, R., Hodgson, D.A., King, J.C., Pudsey, C.J. & Turner, J. 2003. Recent rapid regional climate warming on the Antarctic Peninsula. *Climatic Change*, **60**, 243–274.

Verleyen, E., Hodgson, D.A., Gibson, J., Imura, S., Kaup, E., Kudoh, S., De Wever, A., Hoshino, T., McMinn, A., Obbels, D., Roberts, D., Roberts, S., Sabbe, K., Souffreau, C., Tavernier, I., van Nieuwenhuyze, W., van Ranst, E., Vindevogel, N. & Vyverman, W. 2012. Chemical limnology in coastal East Antarctic lakes: monitoring future climate change in centres of endemism and biodiversity. *Antarctic Science*, **24**, 23–33.

Vincent, W.F. & Howard-Williams, C. 1994. Nitrate-rich inland waters of the Ross Ice Shelf region, Antarctica. *Antarctic Science*, **6**, 339–346.

Vincent, W.F. & Laybourn-Parry, J. 2008. *Polar lakes and rivers*. Oxford: Oxford University Press, 327 pp.

Webster-Brown, J., Gall, M., Gibson, J., Wood, S. & Hawes, I. 2010. The biogeochemistry of meltwater habitats in the Darwin Glacier region (80°S), Victoria Land, Antarctica. *Antarctic Science*, **22**, 646–661.

Whitham, A.G., Ineson, J.R. & Pirrie, D. 2006. Marine volcaniclastics of the Hidden Lake Formation (Coniacian) of James Ross Island, Antarctica: an enigmatic element in the history of a back-arc basin. *In* Francis, J.E., Pirrie, D. & Crame, J.A., *eds. Cretaceous–Tertiary high latitude palaeoenvironments, James Ross Basin, Antarctica*. Geological Society, London, Special Publication, **258**, 21–47.