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Chemical and algal relationships in a salinity series of Ethiopian inland waters

R. B. Wood[1] & J. F. Talling[2]
[1]*Limnology Laboratory, University of Ulster, Magherafelt, Co. Derry, N. Ireland*
[2]*Freshwater Biological Association, Ambleside, Cumbria, U.K.*

Abstract

Most Ethiopian lakes are parts of closed drainage systems and collectively form an extensive salinity series, here treated comparatively for geographical, chemical and algal characteristics. Chemical data are presented for 28 lakes and numerous inflows, including original analyses for 15 lakes, in which total ionic concentration and electrical conductivity vary over 4 orders of magnitude. The principal determinant of a lake's position in the series is the open or closed nature of its individual drainage. At present there are three major closed systems (Awash R. – Afar drainage, northern rift lakes, southern rift lakes), numerous crater lakes with seepage -in and -out, and two cryptodepressions with marine inputs. Salinity is primarily determined by evaporative concentration, enhanced in lakes associated with past marine influence or recent volcanic activity by readily soluble materials in the catchment, and by some thermal-reflux pathways. However, anomalously dilute closed lakes exist, indicative of other processes of solute loss (e.g. past basin overflow, 'reverse weathering', seepage-out).

There are strong positive correlations between increasing salinity and the concentrations of Na^+, alkalinity and Cl^-. The last is used, in conjunction with other analyses of atmospheric precipitation, to estimate the marine and denudative contributions and the evaporative concentration factor, and to distinguish trends of ionic species during evaporative concentration. With several exceptions, affected by past penetration of sea water into the Danakil and L. Assal cryptodepressions, the most saline lakes are soda lakes with $HCO_3^- + CO_3^{2-}$ and Na^+ predominant and Ca^{2+} and Mg^{2+} largely eliminated. Soluble reactive silicate and phosphate tend to increase in concentration along the salinity series, but the unknown dynamics of algal growth are likely to introduce variance. Concentrations in some lakes are extremely high, e.g. > 40 mg SiO_2 l^{-1} and > 1 mg PO_4-P l^{-1}.

Phytoplankters recorded from individual lakes are tabulated and where available the community biomass concentration as chlorophyll *a* is given. Lakes of high salinity-alkalinity are typically very productive in terms of phytoplankton biomass and photosynthetic rates (exceptions: the very deep L. Shala and the very saline L. Abhe), supported in part by relatively high concentrations of phosphorus and inorganic carbon. Many species are of restricted salinity-alkalinity range, being characteristic of waters where levels are low (e.g. desmids, *Melosira spp.*), intermediate (e.g. *Planctonema lauterborni*), or high (e.g. *Spirulina platensis*). Phytoflagellates are most strongly represented in waters with higher concentrations of the bivalent cations Ca^{2+} and Mg^{2+}. The common cyanophyte *Microcystis aeruginosa* can tolerate a wide salinity range, here as elsewhere.

Introduction

Ethiopia contains some 7000 km^2 of inland water bodies whose scientific interest is largely unexploited, notwithstanding the role which such waters might play in ameliorating the effects of drought and protein shortage and do play in sustaining water-borne diseases. With the exception of L. Tana, the lakes described in this paper (which includes all the large lakes) are within closed drainage systems, although several are individually open systems. In consequence a wide range of salinities is represented.

Chemical and related biological features of Ethiopian waters have been reported in the literature over more than 50 years, but study has, overall, not been systematic nor sustained. It has derived mostly from expeditions or short-term residents, although the increasing number of contributions involving Ethiopian workers (e.g. Teferra, 1980; Tedla & Meskel, 1981; Belay & Wood, 1982, 1984; Wodajo & Belay, 1984) including some pathobiology (Kloos & Lemma, 1977; De Sole, Lemma & Mzengia, 1978), are signs of change.* Other relevant publications containing chemical information or related hydrobiology include Omer-Cooper (1930); Morandini (1940); De Filippis (1940); Bini (1940); Brunelli & Cannicci (1940, 1941); Vatova (1940, 1941); Loffredo & Maldura (1941); Cannicci & Almagià (1947); Riedel (1961, 1962); Talling & Talling (1965); Baxter, Prosser, Talling & Wood (1965); UN (1965); Talling & Rzóska (1967); Prosser, Wood & Baxter (1968); Martini (1969); Lloyd (1971); Talling, Wood, Prosser & Baxter (1973); Gonfiantini, Borsi, Ferrara & Panichi (1973); Gasse (1975a, b, 1977); Wood, Prosser & Baxter (1976); Talling (1976); Klein (1977); Hopson (1982); Gasse, Talling & Kilham (1983); von Damm & Edmond (1984); and Wood, Baxter & Prosser (1984). Studies on related aspects of geology and historical lake levels include Mohr (1960, 1961, 1962a, b); Baker, Mohr & Williams (1972); Grove & Goudie (1971); Gasse, Fontes & Rognon (1974); Gasse & Street (1974a, b); Grove, Street & Goudie (1975); Geze (1975); Williams, Bishop, Dakin & Gillespie (1977); and Gasse, Rognon & Street (1980). To these are related other studies of lake history by Gasse (1974a, b, 1975, 1977, 1980) and Gasse & Delibrias (1976) using diatoms as indicators.

The published data on the chemical composition of Ethiopian freshwaters have not been subjected to a modern overview, although Talling & Talling (1965) and Cerling (1979) have set such information from some Ethiopian lakes in a wider African context. The present aim is to bring together a fuller and updated group of records, many of them original. Arranging the lake waters in a series of ascending salinity, we explore relationships between salinity and types of drainage basins, major ionic composition, concentrations of major nutrients, and some qualitative and quantitative characteristics of the phytoplankton.

Geographical features

A dominating feature of Ethiopian geography (Fig. 1) is the Ethiopian Rift Valley which divides the highlands of central Ethiopia before it widens and falls to and below sea level in the Afar Depression, from which rifting continues in two arms as the Red Sea and the Gulf of Aden. Much of the Ethiopian land mass is plateau between 1500 and 3000 m above sea level, with the Simien (to the north-west) and the Bale (to the south-west) mountains rising to over 4600 m and 4300 m respectively. Drainage from these uplands leads to the three major river systems of the Blue Nile (to the north-west), the Awash (north-eastwards), and the Omo (southwards). The rift valley floor, along which many of the lakes are aligned (Fig. 2a), slopes from around 1660 m (L. Galilea) south of Addis Ababa, to about 365 m (L. Turkana) at the Ethio-Kenyan border. Grove *et al.* (1975) and Gasse & Street (1978b) give a general geographical description. North-eastwards from the reservoir L. Galilea the land drops very steeply, and a number of small lakes including L. Metahara (= Besaka) and L. Hertale are strung along the valley of the Awash River, which ends in series of lakes (e.g. L. Gamari, L. Abhe) and saline swamps in the Afar Depression on the Ethio-Djibouti border (Fig. 2b). Some intermediate relief divides these from L. Assal in a cryptodepression (−155 m) over the border near the Red Sea.

Another group of saline lakes (e.g. L. Afrera = L. Giulietti, at −80 m; L. Assale) lies in the Danakil Depression which extends to 100 m below sea level in Tigre Province. A number of small lakes exist high in the Bale mountains, and include L. Orgona and Garba Guratch – an example of a glaciated cirque lake. The western highlands, dominated by the Si-

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* Ethiopian suggestions for improved transliteration include Zwai (for Zwei), Abijata (for Abiata), and Kilole (for Kilotes).

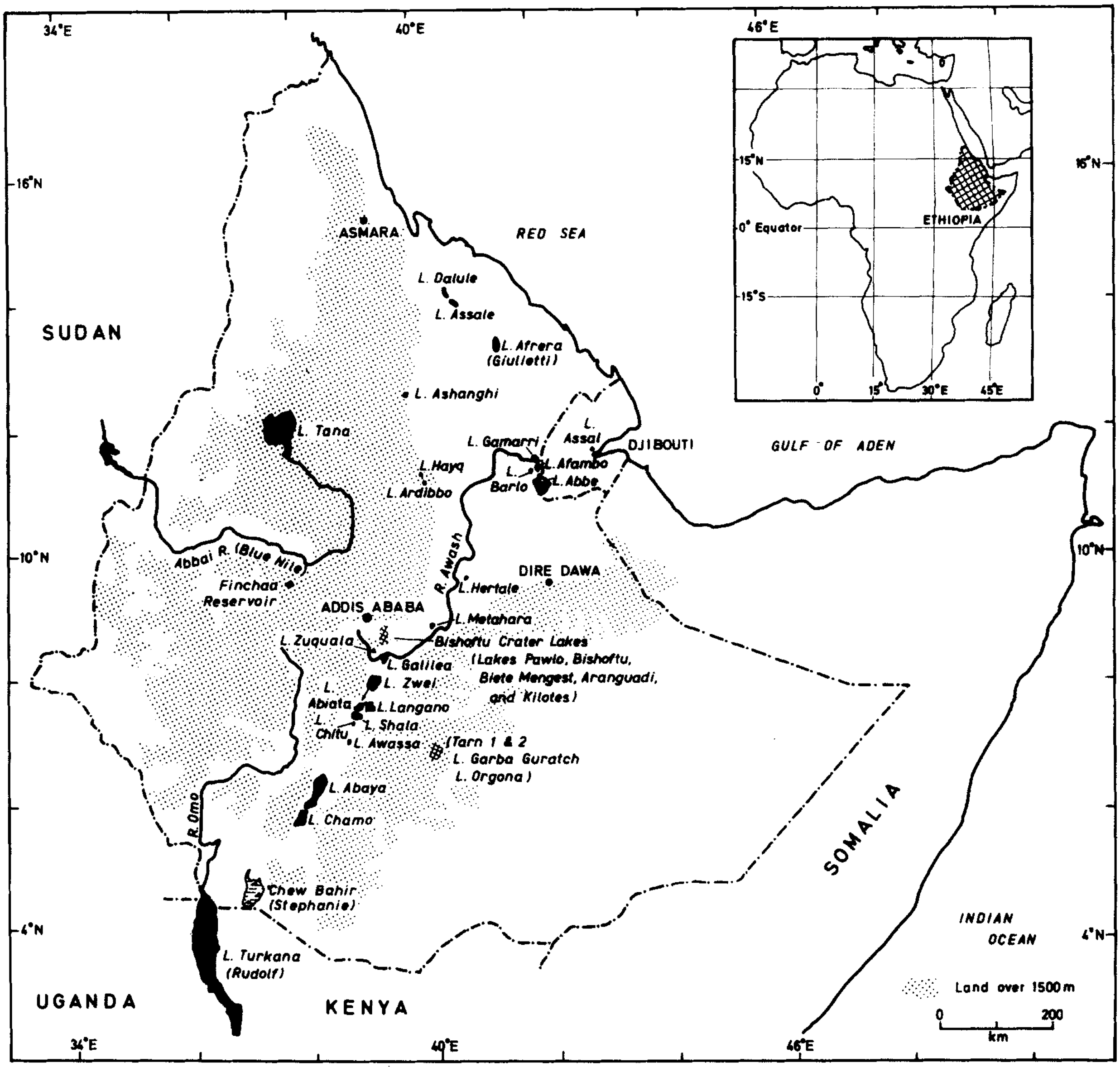

Fig. 1. The location of the principal lakes in Ethiopia.

mien mountains, have the large L. Tana at 1820 m, which is the source of the Abbai River – the Blue Nile, the three lakes (L. Hayq, L. Ardebo and L. Ashanghi) which are found near the edge of the western escarpment of the rift valley at altitudes between 2000 and 2500 m, and the impounded Finchaa Reservoir.

The geology of the Ethiopian Rift system is described by Mohr (1962a, b), Di Paola (1972), Baker *et al.* (1972), and Gasse & Street (1978b). Beadle (1981) reviews briefly the rift origins, former extent, drainage and evolution. Volcanic and tectonic activities are not infrequent and a number of hot springs provide inputs to lakes; exploitation of freshwater geothermal resources has been considered (UN 1973). Crater-lakes are widespread; examples are found on isolated volcanoes (L. Zuquala), the high plateau (Bishoftu group), and in the rift valley (L. Chitu). As the lakes of Ethiopia extend over some 11 ° of latitude and approximately 4100 m of altitude

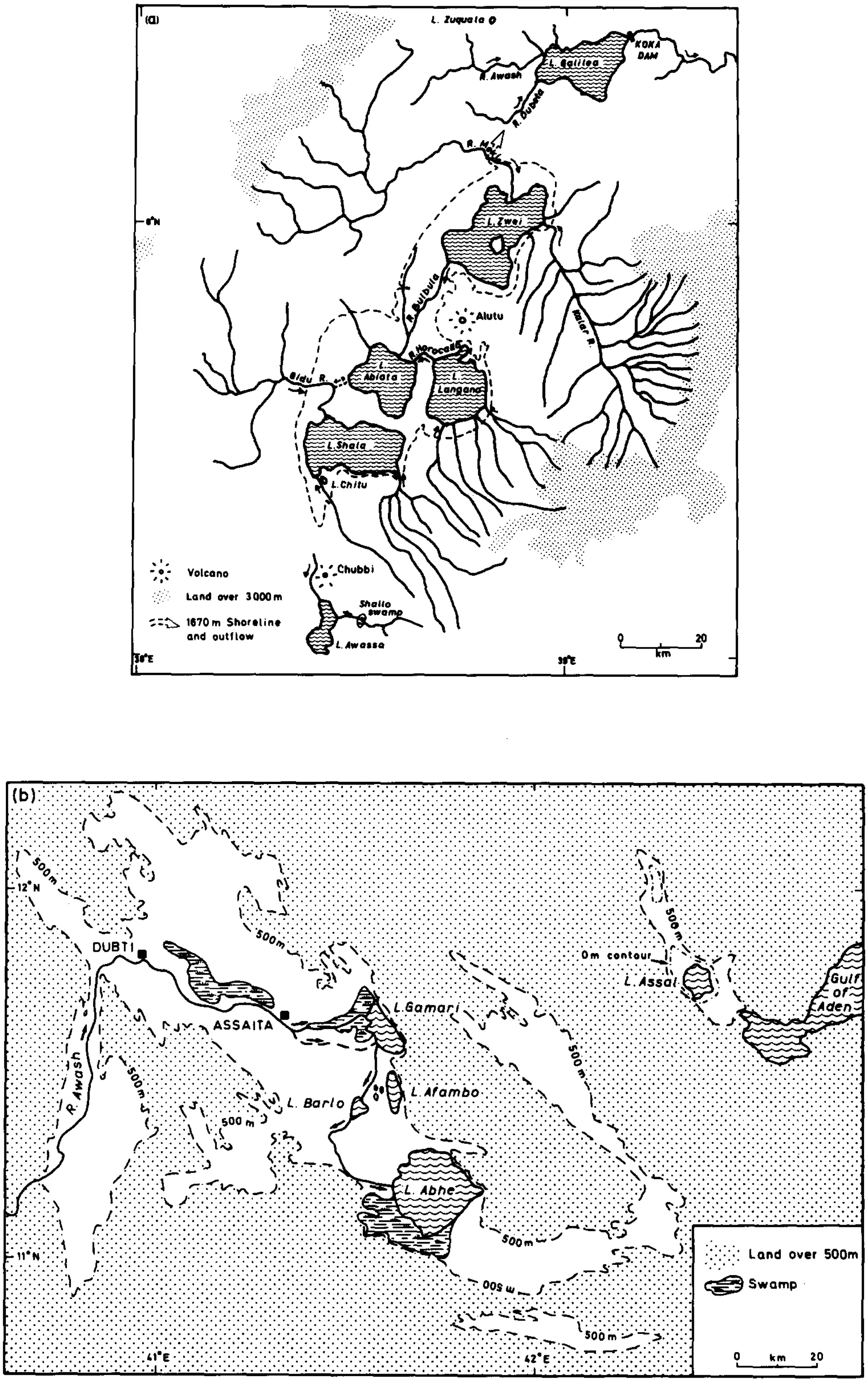

Fig. 2. Drainage systems associated with (a) the Galla lakes of the northern Rift Valley (b) lakes of the terminal R. Awash drainage of the Central Afar region. In (a) the maximum limit at 1670 m altitude of a larger pluvial lake, and its outflow channel, are indicated.

Table 1. Altitude, morphometric characteristics, and salinity of lakes in Ethiopia and adjacent regions. Crater lakes are indicated by asterisks.

Lake	Altitude (m)	Surface area (km^2)	Max. depth (m)	Mean depth (m)	Volume (km^3)	Salinity ($g\ l^{-1}$)
Orgona	~4000	2.5	0.45	-	-	0.711
Garba Guratch	~4000	0.2	-	-	-	0.060
* Zuquala	~2745	~0.5	-	-	-	0.219
Ashanghi	2409	14.9	25.5	14.2	0.212	1.2
Hayq	2030	23	88.2	37.4	0.87	0.771
* Kilotes = Kilole	2000	0.77	6.4	2.6	0.002	5.731
* Bishoftu	1870	0.93	87	55	0.052	1.92
* Aranguadi	1900	0.54	32	18.5	0.010	5.541
* Pawlo	1870	0.58	65	38	0.022	0.928
* Biete Mengist	1850	1.03	38	17.5	0.018	2.565
Tana	1820	3156	14.1	9	28	0.143
Awassa	1680	129	21.6	10.7	1.34	1.008
Galilea (Koka Res.)	1660	~200	-	-	-	0.319
Zwei (Ziway)	1636	442	8.95	2.5	1.6	0.349
* Chitu	1600	0.8	20.5	-	-	38.3
Langano	1582	241	47.9	17	5.3	1.88
Abiata = Abijata	1578	176	14.2	7.6	1.1	16.2
Shala	1558	329	266	87	36.7	21.5
Abaya (Margherita)	1285	1162	13.1	7.1	8.2	0.771
Chamo	1233	551	13	-	-	1.099
Metahara (Besaka)	~1200	3.2	-	-	-	56.3
Chew Bahir (Stephanie)	520		ephemeral			
Turkana (Rudolf)	365	7500	120	33	245	2.894
Gamari	339	70	-	-	-	0.663
Abhe	240	350	37	8.6	3	160
Afrera (Giulietti)	-80	70	>80	-	-	158
Assal	-155	55	40	-	-	276.5

(Table 1), they experience a wide range of climate, accentuated by the annual north-south movements of inter- and sub-tropical frontal zones across the country. Typically wet and dry seasons alternate. Predominantly south-western winds bring the bulk of the rain and associated high relative humidity in July and August over much of the Ethiopian plateau; the L. Tana region receives c. 1200 mm average long-term annual rainfall, and the high Bale mountains perhaps 1500 mm. The more northerly rift lakes might receive up to 600 mm in a normal year, falling to about 200 mm at L. Turkana and to nearer 100 mm in the Afar depression (Wood & Lovett, 1979). Both local variations and the widely reported droughts of the early 1980's make these generalities of limited value. However both the Rift and Afar are regions of rainfall deficit, with evapotranspiration greater than a mean annual rainfall, 'so that the existence of present-day lakes is directly dependent on inflows from the surrounding highlands' (Gasse & Street, 1978b).

Methods

Water samples for analysis were taken using either a clear plastic 1-litre Ruttner sampler or an opaque 5-litre Van Dorn sampler, transferred to opaque plastic containers and transported to the laboratory as soon as possible. All analyses from the Bishoftu crater lakes could be begun within a few hours of sampling. Delay during longer field trips was unavoidable although samples taken in 1966 were cooled in a portable gas-powered refrigerator. Except where otherwise stated analyses are of surface water taken at 0.1 – 0.5 m depth.

Table 2. The chemical composition of lake surface waters in Ethiopia and immediately adjacent areas.

	Reference	Date	Conductivity k_{20} (μS cm^{-1})	Salinity (g l^{-1})	(meq l^{-1})									SiO$_2$ (mg l^{-1})	PO$_4$·P (μg l^{-1})	pH	Alk/Cl	$\frac{(Ca+Mg)}{(Na+K)}$
					Σcat	Σan	Na$^+$	K$^+$	Ca^{2+}	Mg^{2+}	HCO$_3^-$ + CO$_3^{2-}$	Cl$^-$	SO$_4^{2-}$					
Tarn 2 (Bale Mts.)	Löffler (1978)	Apr. '76	54.1	0.040	0.54	0.54	0.01	0.027	0.30	0.11	0.30	0.084	0.16			6.2	3.57	2.38
Tarn 1 (Bale Mts.)	Löffler (1978)	Apr. '76	57.1	0.039	0.44	0.58	0.13	0.014	0.14	0.16	0.4	0.109	0.07			6.45	3.67	2.14
Garba Guratch	Löffler (1978)	Apr. '76	131	0.060	0.79	0.79	0.29	0.019	0.23	0.25	0.6	0.050	0.14			7.4	12	0.52
Tana	Original	Mar. '64	137	0.143	1.68	1.62	0.24	0.040	0.945	0.45	1.52	0.044	0.052	14.5	30	8.4	34.5	5.0
Zuquala*	Wood (1971)	Jan. '67	(238)	0.219	2.69	2.93	0.83	0.56	0.62	0.68	2.1	0.83	<0.1			7.5	2.53	0.94
Galilea (Koka Res.)	Original	Mar. '64	274	0.319	3.66	3.62	1.06	0.17	1.70	0.72	3.22	0.16	0.24	32			20.13	1.98
Zwei	Talling & Talling (1965)	May '61	370	0.431	4.46	4.82	2.78	0.36	0.51	0.82	3.92	0.51	0.6	47			7.69	0.42
	Original	Mar. '64	322	0.349	3.72	3.80	2.11	0.30	0.70	0.615	3.34	0.24	0.22	45		8.9	13.92	0.55
Orgona	Löffler (1978)	Apr. '76	718	0.711	10.54	10.27	2.86	0.371	3.78	3.53	5.5	4.089	0.68			8.2	1.35	2.26
Hayq*	Baxter & Golobitsh (1971)	Apr. '69	750	0.771	10.2	10.3	3.3	0.30	1.0	5.6	8.9	1.2	0.18	2	131	9.0	7.42	1.83
Awassa*	Talling & Talling (1965)	May '61	1050	1.063	12.0	12.0	10.22	1.15	0.22	0.39	10.5	0.96	0.56	72			10.94	0.05
	Original	Mar. '64	840	1.008	11.2	11.04	9.48	1.04	0.58	0.10	9.3	0.84	0.90	96	<5	8.8	11.07	0.06
Abaya (= Margherita)	Talling & Talling (1965)	May '61	900	0.884	10.5	10.6	8.96	0.41	0.61	0.48	8.5	1.49	0.58	45			5.70	0.12
	Original	Jan./Feb. '64	623	0.771	9.1	9.1	7.70	0.41	0.76	0.22	7.41	1.10	0.60	40	128	8.9	6.74	0.12
	Belay & Wood (1982)	July '66	953	0.868	9.8	10.5	8.48	0.36	0.75	0.21	8.4	1.35	0.69	48	30	8.9	6.22	0.11
Chamo*	Original	Feb. '64	1100	1.099	13.6	13.5	11.6	0.51	0.70	0.75	10.9	2.0	0.60	28			5.45	0.12
	Belay & Wood (1982)	July '66	(1000)	0.945	10.8	11.7	9.1	0.36	0.7	0.64	9.4	1.66	0.62	38	14	8.9	5.66	0.14
Pawlo*	Prosser et al. (1968)	Apr. '63	(1000)	0.928	11.7	11.1	5.5^x	1.05^x	0.55	4.65	10.2	0.9	<0.1	38	<5 – 100	9.2	11.33	0.79
	Original	Apr. '64							0.46	4.87	10.8	0.79		77	<5		13.67	
Gamari*	Gasse (1975)																	
	Gasse et al. (1983)	Dec. '72	1300	0.701	9.19	8.48	6.09	0.28	1.91	0.91	6.05	1.56	0.88	35		8.0	3.88	0.44
Ashanghi*	Loffredo & Maldura (1941)	'37	1530	1.2														
Langano	Talling & Talling (1965)	May '61	1900	1.786	22.7	22.5	21.74	0.71	0.12	0.23	15.0	6.08	1.42	54			2.47	0.02
	Original	Feb./Mar. '64	1810	1.88	20.5	20.9	19.6	0.67	0.28	<0.1	14.4	4.7	1.8	48	90	9.4	3.06	0.02
	Baumann *et al.* (1975)	May '71		1.700	25.55	21.9	23.9	0.33	0.54	0.17	13.61	7.52	0.77			9.2	1.81	0.03
Bishoftu*	Prosser *et al.* (1968)	Apr. '63	(1830)	1.920	23.61	24.7	16.0^x	1.5^x	0.37	5.8	20.0	4.0	0.35	38	<5 – 100	9.2	5.0	0.35
	Original	Mar. '64							0.35	6.44	19.3	3.49	–	38	<5			

Table 2. Continued.

	Reference	Date	Conductivity k_{20} (μS cm^{-1})	Salinity (g l^{-1})	(meq l^{-1})									SiO$_2$ (mg l^{-1})	PO$_4$·P (μg l^{-1})	pH	Alk/Cl	$\frac{(Ca+Mg)}{(Na+K)}$
					Σcat	Σan	Na$^+$	K$^+$	Ca^{2+}	Mg^{2+}	HCO$_3^-$ + CO$_3^{2-}$	Cl$^-$	SO$_4^{2-}$					
Biete Mengest*	Prosser *et al.* (1968)	Apr. '63	(2340)	2.565	29.5	32.9	23.9^x	1.31^x	0.34	3.94	26.8	5.67	0.4	55	<5	9.2	4.73	0.17
Turkana (= Rudolf)*	Talling & Talling (1965)	Jan. '61	3300	2.894	36.2	39.3	35.22	0.54	0.29	0.25	24.5	13.38	1.40	18			1.83	0.015
	Hopson (1982)	Aug. '73	3071	3.017	42.4	40.2	41.4	0.63	0.21	0.28	24.2	13.8	1.2	18	277	9.2	1.75	0.012
	Yuretich & Cerling (1983)	1973 – 5	(2630)	2.434	33.6	33.4	32.7	0.52	0.23	0.19	19.5	12.6	0.8	19.8		9.2	1.55	0.013
Kilotes = Kilole*	Prosser *et al.* (1968)	Apr. '63		5.731	75.7	77.4	70.5^x	4.5^x	0.7	<0.6	63.4	13.6	0.4	32	4800 – 5500	9.6	5.7	0.016
	Original	Mar. '64	5930			81.6	71.0	4.9			66.6	11.5	3.5	45	7000		5.79	
Aranguadi*	Prosser *et al.* (1968)	Apr. '63		5.144	75.7	74.1	67^x	8.1^x	0.67	<0.6	51.4	22.0	0.7	50	2400 – 4100	10.3	3.4	0.016
	Original	Feb. '64	6000	5.541	76.1	79.9	65.3	9.6	0.7	0.5	57.2	17.1	5.6	50	3200		3.35	0.016
Abiata*	Talling & Talling (1965)	May '61	30000	20.117	285	316	277.2	8.5	<0.15	<0.6	210	91.3	15.0				2.30	
	Original	Mar. '64	15800	16.2	228.5	240.5	222	6.5	<0.1	<0.1	166.5	51.5	22.5	128	50	10.3	4.7	0.004
Shala*	Talling & Talling (1965)	May '61	29500	19.582	278	306	271.7	6.5	0.15	0.6	200	93.0	13.5	130			2.15	
	Original	Mar. '64	19200	21.5	308	316	301	7.1	<0.1	<0.1	212	79	25.0	112	760	9.9	3.92	0.003
	Baumann *et al.* (1975)	May '71		16.8	261	191	256.5	2.87	0.25	0.06	188	78.5	2.98			10.0	2.39	0.001
Chitu*	Original	Aug. '66	28600	38.3	556	539	539	17.2	<0.1	<0.1	400	121	17.7	320	1700	9.8	4.46	0.0015
	Baumann *et al.* (1975)	May '71		34.8	619	553.3	608.7	10.5	0.13	0.06	401.6	137	16.7			10.2	2.93	0.003
Metahara*	Talling & Talling (1965)	May '61	72500	56.3	784	831	774	10.4	<0.15	<0.6	580	154.6	97.5			9.9	5.71	0.005
Abhe*	Gasse *et al.* (1974) Gasse & Street (1978b), Gasse (1980)			~160	–	2562	2390	–	–	–	1059	1149	354	416	–	10.3	0.92	–
Afrera (= Giulietti)*	Martini (1969)	Feb. '68	250000	159	2846	2676	1930	71	770	75	2.2	2650	24	74	–	6.55	0.0008	0.42
	Gonfiantini *et al.* (1973)	Dec. '69			2855	–	1817	69	878	91	–	2670	27	–	–	–		0.51
Assal TFAI*	Brisou *et al.* (1974)	July '69		276.5	4793	4793	3263	138	725	667	–	4687	48	–	–	–	<0.001	0.41

( ) indicates conductivity values calculated as described in the Methods. * = lakes without an obvious outlet. ^{x} = Na$^+$ and K$^+$ determined in June 1965. All salinity values are calculated by summing the individual constituents except for L. Ashanghi and values from Baumann *et al.* (1975). Where available, original data are used in the construction of Figs. 3 and 5 – 11.

Phytoplankton was generally concentrated for microscopic examination by iodine-sedimentation, or in a few cases preserved with formalin. Net collections were used only for supplementary examinations. For quantitative estimates, samples were filtered through Whatman GF/C glass fibre filters and chlorophyll *a* (uncorrected for degradation products) was determined according to the method of Talling & Driver (1963) using either methanol or acetone as solvent.

Before filtration, pH was taken by glass electrode either in the field on longer collecting trips, or in the laboratory where a more sensitive instrument was available. Values given here are as measured, not air-equilibrium values. Electrical conductivity was measured using a standard electrode system (cell constant 1.00), and all values have been corrected to 20 ° using a temperature coefficient of 2.3% per °C (after Talling & Talling, 1965). Corresponding values for 25 °C, now widely used, would be higher by a factor of 1.12. Conductivity is used as the basis of the salinity series, and where no conductivity measurements were taken (L. Zuquala, L. Pawlo, L. Bishoftu and L. Biete Mengest) values have been determined from regression lines based on total dissolved solids, Σ cations, Σ anions, sodium, and alkalinity, both for the whole series, and for 10 lakes selected to cover as closely as possible the values found in each of the lakes under consideration. Discrepancies between the five methods were small ($<10\%$). Where salinity as total dissolved solids (TDS) was not given by the authors quoted, it has been determined by summing the individual ions and assuming no other major contribution. For the lakes considered here approximate equivalences are: 1 meq l^{-1} total cations or total anions $\simeq 87\ \mu S\ cm^{-1}$ ($r^2 = 0.98$) $\simeq 0.059$ g l^{-1} TDS ($r^2 = 0.99$).

The chemical analyses were carried out using methods described in Talling & Talling (1965), Prosser *et al.* (1968) and Wood *et al.* (1984). Most derive from Mackereth (1963) and Mackereth *et al.*(1978) and in outline are as follows: sodium and potasium by flame photometry; calcium and magnesium by compleximetric titration using ammonium purpurate and Solochrome Black (= Eriochrome Black) as indicators; alkalinity (bicarbonate + carbonate) by titration to pH 4.5 end-point (with probable overestimation by 0.02 meq l^{-1}: Sutcliffe *et al.*, 1982); chloride, and sulphate (with any nitrate), by cation exchange using resin in both silver and hydrogen exchange forms; silicate (expressed as silica, SiO_2) and phosphate by colorimetry or spectrophotometry of their respective molybdate complexes. In the field and during 1964 in the laboratory, silicate and phosphate were measured using a Lovibond 'Nesslerizer' colorimeter (Tintometer Ltd, Salisbury, England) with a light path of 112 mm and standard colour discs calibrated against standard solutions. Possible interference of silicate in the phosphate estimation was avoided by a preliminary dilution of alkaline lake samples, so that the reaction mixture was kept below pH 1.2. Thus the soda-lake Abiata was analyzed as silicate-rich but phosphate-poor. Arsenate interference was assumed negligible.

Methods employed by authors of the other results quoted are given in the appropriate papers.

Salinity series and drainage relationships

Table 2 summarizes information on the chemical composition of 28 lakes, arranged in order of salinity. The salinity series covers almost four orders of magnitude, from 0.04 to 276 g l^{-1}. The ten most saline lakes fall into the definition by Williams (1964) of 'saline lakes', containing in excess of 3 g l^{-1} of total dissolved solids.

Fig. 3 illustrates the relationship between conductivity and total cations, total anions, and salinity as total dissolved solids. Given that there is good agreement between salinity and conductivity, and that many data sets include values for conductivity, the salinity series is discussed below using conductivity as the basis. The mean conductivity per unit ionic content of cations *or* anions is 87 $\mu S\ cm^{-1}$ per meq l^{-1}, close to the mean value (85) that Talling & Talling (1965) calculated for 67 African waters. Such a quotient must inevitably decline at high ionic strength. Within the Ethiopian analyses the change, with increasing salinity, in the dominant ion-species (e.g. from Ca^{2+} to Na^+ – see Figs 6b, 8), does not markedly alter this quantity.

Water input-output relationships are probably the main determinant of the lake status in the salinity series of Table 2. Lakes with no obvious surface outflow, indicated by asterisks, include the twelve most

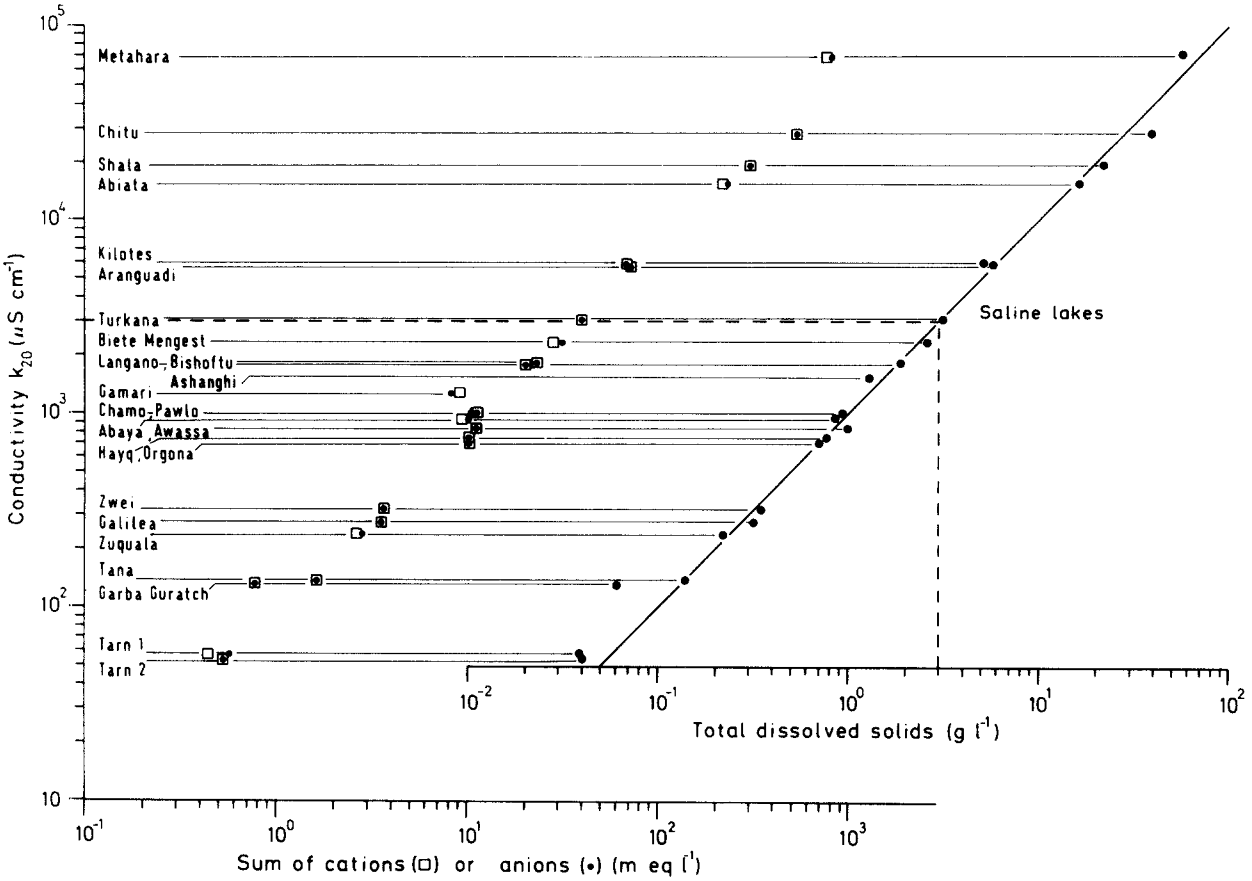

Fig. 3. Variation in concentrations of the sum of cations (□), the sum of anions (●), and salinity as total dissolved solids in surface waters from Ethiopian lakes arranged in order of electrical conductivity. The dashed line in this and Figs.. 5, 6, 8 denotes the 3 g l^{-1} boundary of salinity. The very saline lakes Afrera, Abhe, and Assal are omitted here and in Figs. 5–8.

saline lakes of the series. In this situation, if accompanied by a maintained lake level or lake volume and negligible seepage-out, evaporation loss can balance inflow plus direct precipitation;' with time the lake becomes more saline, the extent depending on the time since the system became closed.

On a small scale, closed drainage appears in numerous crater lakes such as the Bishoftu group and L. Chitu, and in the volcanic lava-dam lake of Metahara (= Besaka). On a large scale it characterizes three lake-systems: the Galla lakes Zwei-Langano-Abiata-Shala of the north Rift region, the lakes Abaya-Chamo-Chew Bahir-Turkana of the south Rift region, and the lakes Gamari-Afambo-Bario-Abhe in the central Afar region fed by the River Awash. These three closed systems are shown in altitudinal and hydrological profile in Fig. 4, together with lakes Assal and Afrera of near-costal cryptodepressions. In terms of salt accumulation Shala, Turkana and Abhe are undoubtedly the main terminal lakes and some upstream lakes with throughput are of relatively low salinity (Zwei, Langano; Gamari; Abaya, Chamo). However there are historical and topographical complications governing solute transfer in each system.

At present, L. Abiata is the final evaporating basin for both L. Langano via the Horocallo River and L. Zwei via the Bulbula River (it requires an approximately 15 m rise in level of Abiata before it overflows via branches of the lower Gidu River into L. Shala). Even at its most dilute, L. Abiata shows a 10 times and 60 times concentration of solutes over L. Langano and L. Zwei respectively (see Table 2), and approximately a 250 times concentration over the

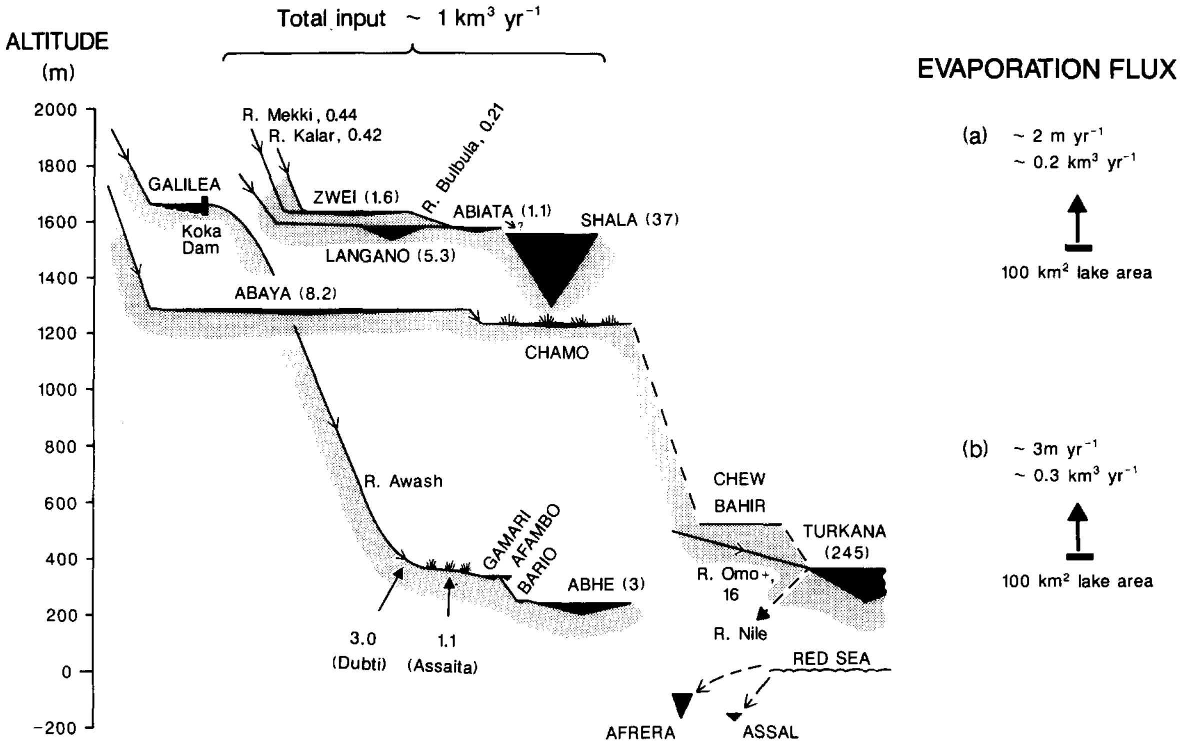

Fig. 4. Diagramatic hydrological sections along three Ethiopian lake-river systems of closed drainage, with common scales of altitude, lake area, and maximum lake depth. Numbers in brackets indicate lake volume in km^3, and other numbers water-flows in km^3 yr^{-1} estimated during 1962–64 (R. Awash), 1969–73 (north Rift system), and 1972–75 (R. Omo – L. Turkana). For comparison rough estimates are given (right) of evaporative water fluxes from a lake area of 100 km^2 situated (a) above 1000 m altitude, (b) below 1000 m altitude. Broken lines show past or intermittent river connexions.

streams draining the Bale mountains. The neighbouring deep L. Shala is of similar salinity yet contains a much greater stock of solutes, for Cl^- amounting to about 97% of the total quantity present in the north Rift system (von Damm & Edmond, 1984). This proportion could not be plausibly supplied by drainage to L. Shala alone, and requires past transfer from L. Abiata by surface or sub-surface channels that are at present uncertain (Grove *et al.*, 1975, von Damm & Edmond, 1984). Over some period before c. 5000 BP the entire lake group was fused as a single large Rift lake with overflow at 1670 m to the River Awash (Fig. 2a), so that most salt accumulation has been in the more recent period (Grove *et al.*, 1975, Gasse & Street, 1978b).

In the south Rift lake system inflow to the terminal L. Turkana has probably long been dominated by the R. Omo, whose present discharge of ~ 14 km^3 yr^{-1} (Yuretich & Cerling, 1983) is an order of magnitude greater than those of the R. Awash and the combined north Rift inflows. Nevertheless discontinuous river flows have in the past linked L. Abaya, L. Chamo, and Chew Bahir to L. Turkana, and that lake to the White Nile. In contrast, the Awash River course is still maintained to the terminal L. Abhe, but lateral spillage and down-seepage to ground water in a swampy region upstream of the lakes (between Dubti and Assaita) much reduces river discharge as from ~ 3 to ~ 1 km^3 yr^{-1} in 1962–4 (Gasse *et al.*, 1974).

The steady-state persistence of a closed-basin lake requires that the annual water inflow should equal the annual evaporation loss minus direct rainfall on the lake. In all three lake systems the last term is less than half the evaporation loss, whose approximate magnitude per 100 km^2 lake area is indicated in Fig. 4 for the higher and lower lakes.

Hydrologically controlled salinization in closed basins can be modified by a number of processes, whose probable application to Ethiopian lakes is outlined below. Their assessment often requires additional information on the chemical composition of inflows (Table 3).

(i) A surface outflow may be present, determining a limited retention time in an open basin and a usually low to moderate salinity related to the geochemistry of the catchment. Thus the chemical composition of water of L. Zwei is almost identical to that of a principal inflow, the Meki River (Makin *et al.*, 1976, von Damm & Edmond, 1984).

(ii) A surface outflow may be present but the water budget of the lake is under direct atmospheric control, with the terms of direct precipitation (P) and evaporation (E) at the lake surface being much larger than those of surface inflow (F_i) and outflow (F_0). If P and E are of similar magnitude, as in a higher rainfall region of Ethiopia, the salinity can be secondarily similar to that of the major inflows. L. Tana is a probable example, although analyses of its inflows are lacking. If $(E-P) > F_0$, and loss by seepage (iv below) and chemical reactions (viii below) can be neglected, the lakewater salinity will stabilize around a value in excess of the average inflow concentration by a factor equal to F_i/F_0. Quantitative examples, including L. Langano, are discussed later.

(iii) A surface outflow may develop only rarely, at exceptional high lake levels. It can account for some anomalous cases of low salinity in normally closed basins. In this context L. Chamo and L. Awassa appear in Table 2. Lake Chamo drains its own catchment and, at times, that of L. Abaya by way of the R. Kulfo. It is not particularly deep (maximum depth <20 m) yet has a conductivity of only about 1000 μS cm^{-1}.

Grove *et al.* (1975) provide an explanation, having shown that irregular overflow of L. Chamo via the Sagan River to the Chew Bahir (= Stephanie) swamp/lake has occurred in the last hundred years.

L. Awassa is the smallest of the major lakes in the Ethiopian Rift Valley, and has a conductivity of only 800–900 μS cm^{-1}. Dilute inflows may have favoured this condition (Table 3). The inflow, which drains the Shallo papyrus-dominated swamp to the north-east of the lake (with a thermal source probably analysed as 'L. Shalafu' in Talling & Talling, 1965) and which was estimated to be contributing some 40% of the total inflow at the time of sampling, had a conductivity of 50 μS cm^{-1} and the other 60% of inflow from 8 other streams averaged around 100 μS cm^{-1}. The more saline hot spring contributed very little and the lake water thus is only about ten times more concentrated than the inflow. There are local reports that, in times of high rainfall, there is an outflow from the southern end of L. Awassa. However, we found no clear evidence of this, and from local topography it is hard to imagine a water-course unless underground. Grove *et al.* (1975) also reported no surface outflow.

(iv) A 'closed' lake-basin may have appreciable seepage-out and hence a lower salinity than otherwise expected. Good African examples elsewhere are lakes Naivasha (Gaudet & Melack, 1981) and Chad (Carmouze, 1983). The crater lake Zuquala (photograph in Omer-Cooper, 1930) is almost certainly an Ethiopian example, with notably low salinity – although direct measurements of seepage are lacking. A varying amount of seepage-out probably also accounts in large part for the wide range of salinity in members of the Bishoftu crater lakes (Pawlo, Biete Mengest, Bishoftu, Kilotes, Aranguadi), all of which lack surface outflows, have very small catchments but receive transitory spring and seepage-in water of low salinity. Seepage-out may also underlie the anomaly of L. Awassa discussed in (iii) above.

(v) Saline inflows will tend to produce a lake water of higher salinity than might be expected from its water-budget. Varied expressions are seen in the more saline open Ethiopian lakes, of conductivity greater than 600 μS cm^{-1}. Thus the mountain lake Orgona (718 μS cm^{-1}) receives drainage from an adjacent area of alkaline trachyte (Löffler, 1978). L. Gamari in the low-lying Afar region receives a single major inflow from the Awash River, which is near the end of its course and already of considerable salinity (Table 3). L. Abaya (= Margherita) was shown by von Damm & Edmond (1984) to be of similar salinity to its main inflow, the R. Bilate. However the analyses of Klein (1977), partly reproduced in Table 3, illustrate the variability and local influence of spring water. Site A in the south-west of the lake is close to the areas sampled by van Someren (Talling & Talling, 1966), by us in 1964 and 1966, by von

Table 3. The chemical composition of some Ethiopian lakes and their inflows.

Lake	Input (Date)	{Reference}	Conductivity k_{20} (μS cm^{-1})	(meq l^{-1})									SiO$_2$ (mg l^{-1})	PO$_4$·P (μg P l^{-1})	pH
				Σcat	Σan	Na$^+$	K$^+$	Ca^{2+}	Mg^{2+}	Alk	Cl$^-$	SO$_4^{2-}$			
Hayq	(April '69)	{1}	750	10.2	10.3	3.3	0.3	1.0	5.6	8.9	1.2	0.18	2	131	9.0
	R. Anchercah		460	5.7	6.0	1.2	0.07	1.1	3.5	5.4	0.21	0.39	20	44	-
Awassa	(Aug. '66)	{2}	882	9.18	11.1	7.62	0.85	0.2	0.26	9.6	0.92	0.61	130	8	9.2
	8 small streams (~60%)		106 (62–198)	1.24	1.43	0.57	0.11	0.26	0.30	1.17	0.14	0.12	88	45	8.2
	Hot spring		1924	25.0	34.3	23.5	1.1	0.28	0.11	26.0	3.8	3.7	150	80	8.0
	Swamp (~40%)		48	0.46	0.68	0.14	0.05	0.1	0.10	0.45	0.13	0.1	80	<5	7.8
Abaya (A)	(Feb. '75)	{3}	820	10.1	10.4	8.5	-	-	-	6.3	1.5	0.8	-	-	8.9
	Spring (C)		2200	25.5	26	22.8	-	-	-	18.1	1.7	0.3	-	-	6.9
	Beach Spring (D)		640	6.5	6.6	5.1	-	-	-	0.2	0.3	4.0	-	-	6.4
	Hot Spring (E)		6100	62.4	62.7	56.5	-	-	-	46	20.7	2.3	-	-	9.4
Abaya (B)			1400	16.5	16.3	14.4	-	-	-	10.6	2.1	1.5	-	-	8.6
Abaya	(Jan.–Feb. '76)	{4}		10.22	9.17*	8.78	0.42	0.74	0.28	7.44	1.27	0.12	43.2	-	8.85
	R. Bilate			7.80	8.05*	6.56	0.50	0.46	0.28	6.13	0.40	0.98	46.3	-	8.80
	R. Humasa			2.04	1.70*	0.80	0.30	0.64	0.30	1.48	0.11	0.072	45.1	-	7.85
Gamari	(Dec. '72)	{5}		9.19	8.48	6.09	0.28	1.91	0.90	6.05	1.56	0.88	35	-	8.0
	R. Awash at Assaita			6.04	5.86	3.39	0.18	1.88	0.59	4.57	0.93	0.36	32	-	7.5–8.0
Langano	(Jan. '64)	{2}	1810	20.3	20.8	19.3	0.64	0.15	0.22	14.3	4.7	1.8	64	-	-
	Hot Spring		3200	34.8	35.8	33.7	1.1	-	-	14.7	13.7	7.4	72	-	-
Langano	(Aug. '66)	{2}	2180	20.03	21.56	19.1	0.58	0.12	0.09	15.0	5.3	1.26	96	72	9.2
	7 Rivers – mean		51 (39–71)	0.65	0.75	0.16	0.09	0.30	0.1	0.54	0.14	0.07	20	12	7.8
	Hot Spring		2110	26.75	35.2	25.5	1.0	0.12	0.13	15.1	12.6	7.5	190	103	9.1
	Hot Spring Bay		2560	19.58	22.2	18.7	0.6	0.14	0.14	15.0	5.3	1.97	98	68	9.2
Langano	(Jan.–Feb. '76)	{4}		21.48	20.07*	20.58	0.68	0.13	0.09	13.59	5.2	0.4	50.6	-	8.8
	4 Rivers – mean			1.73	1.60	0.67	0.22	0.60	0.24	1.42	0.05	0.08	53.7	-	7.76

Table 3. Continued.

Lake	Input (Date)	{Reference}	Conductivity k_{20} (µS cm^{-1})	(meq l^{-1})									SiO_2 (mg l^{-1})	$PO_4 \cdot P$ (µg P l^{-1})	pH
				Σcat	Σan	Na^+	K^+	Ca^{2+}	Mg^{2+}	Alk	Cl^-	SO_4^{2-}			
Turkana	(1973 – 76) – mean	{6}		33.7	33.4*	32.74	0.51	0.23	0.19	19.5	12.56	0.83	19.8	-	9.2
	R. Omo			1.23	-	0.42	0.05	0.47	0.29	-	0.08	-	-	-	7.0
	R. Kerio			3.72	3.62*	1.29	0.15	1.33	0.48	2.84	0.42	0.17	-	-	7.8
	R. Kerio (15%)/R. Omo (85%) weighted average			1.53	1.77*	0.57	0.06	0.59	0.31	1.4	0.14	0.17	20	-	7.1
Abiata	(Oct. '66)	{2}	21000	265.7	305.2	260	5.3	0.06	0.06	215	75.2	15.0	-	-	10.3
	R. Bulbulla		276	4.7	4.46	2.0	1.4	0.5	0.8	3.46	0.4	0.6	-	-	8.9
	R. Horocallo		2230	21.8	22.9	20.9	0.64	0.11	0.12	16	5.5	1.35	80	88	9.2
Abiata	(Jan. – Feb. '76)	{4}		198.9	192.4*	193.9	4.91	0.08	0.05	138.1	53.9	0.3	97.6	-	9.6
	R. Bulbulla			3.96	3.61*	2.31	0.29	0.72	0.64	3.19	0.29	0.05	40.3	-	7.6
	R. Horocallo			21.48	20.07*	20.58	0.68	0.13	0.09	13.59	5.2	0.4	50.6	-	8.8
Shala	(Jan. '64)	{2}		311.1	312	304	7.1	<0.1	<0.1	210	77	25	128	700	-
	Hot Spring		8200	111.7	104	111	0.7	<0.1	<0.1	55.6	41.3	7.5	112	-	-
Shala	(Oct. '66)	{2}	22000	300.8	317.4	295.7	5.1	0.06	0.06	216	87.9	13.5	-	-	9.9
	9 Rivers – mean		68 (52 – 81)	0.83	0.95	0.26	0.09	0.24	0.24	0.66	0.16	0.13	52	4	8.0
Shala	(Jan. – Feb. '76)	{4}		312.6	322.9*	305.3	7.04	0.19	0.08	218.8	90.28	3.24	120.2	-	9.6
	R. Adabat			2.97	2.66*	1.59	0.32	0.76	0.3	1.99	0.38	0.24	80.5	-	7.6
	R. Gidu			3.18	-	2.21	0.69	0.28	0.4	2.96	0.23	-	-	-	-

References: Data from {1} Baxter and Golobitsh (1970)
{2} Original
{3} Klein (1977)
{4} Von Damm and Edmond (1984)
{5} Gasse (1975)
{6} Yuretich and Cerling (1983)

* includes measured fluoride.

Damm & Edmond (1984) and by Belay (Belay & Wood, 1982). The overall salinity is similar for all the analyses (see Table 4). Klein's Site B was in the north-west of L. Abaya and close to the spring (C), the beach spring (D) and the fumarole hot spring (E) whose relative discharges were 12, 1 and 15 l sec^{-1} respectively. The major ion analyses of those waters are given in Table 3 where the wide differences may be noted, together with the effect which the more saline inputs have on the lake water at site B.

(vi) A reflux pathway may exist, with lake water seeping down as groundwater, heating geothermally, and rising under pressure as hot spring inputs. Hot springs are widespread around Ethiopian lakes and many are saline when in or near basins of closed drainage. Such a closed circulatory path, with lake acting as an evaporating pan above, is a factor in the salinization of several rift lakes in Tanzania (Guest & Stevens, 1951) and Kenya (Baker, 1958; Eugster, 1970). Besides promoting evaporation without new input, the groundwater-spring systems may serve to transfer solutes laterally between nearby basins. In the north Rift lakes the water discharges involved are inconsiderable compared to other fluxes, but salinity can be high (a hot spring inflow to L. Shala had a conductivity value of 8200 $\mu S\ cm^{-1}$ in 1964: Table 3) and salt transfer possibly appreciable. Evidence for vertical recirculation from parent lakewater is provided by similarities of gross chemical composition (Table 3, and Baumann *et al.*, 1975) and isotopic evidence from ^{18}O values (Craig, 1977, quoted by von Damm & Edmond, 1984). For L. Afrera in the Danakil depression there is similar evidence from ionic composition and $\delta^{18}O$ and δD values (Gonfiantini *et al.*, 1973). Without such evidence it is often difficult to distinguish between saline springs as new chemical inputs or as recirculation pathways. The isotopic evidence by Gonfiantini *et al.* (1983) also showed similarities to marine (Red Sea) brine. A modern ingress of sea water by seepage does occur to the saline L. Assal only 10 km from the Red Sea but 155 m lower.

(vii) Differences of solubility between carbonate-bicarbonate and chloride salts can influence the higher salinity levels. The predominance of chloride in L. Assal makes possible the very high salinity ($\sim 300\ g\ l^{-1}$) of this lake.

(viii) Some chemical transformations in and around a lake may reduce salt content and salinity. Even at relatively low salinity precipitation of calcite ($CaCO_3$) can be inferred (p. 46) and is a significant component of many Ethiopian lake sediments (e.g. Shala: Bauman *et al.*, 1975; Turkana: Yuretich & Cerling, 1983; L. Gamari: Gasse *et al.*, 1974). Precipitation of trona ($Na_2CO_3 \cdot NaHCO_3 \cdot 2H_2O$) is often well-marked around the margins of L. Abiata, depending on water-level. 'Reverse weathering' in lake sediment-solute systems was postulated from mass balance considerations as a solute sink for some Ethiopian rift lakes by von Damm & Edmond (1984), although the hydrological information appears too rough for certainty. It involves a sediment transformation (neoformation of smectites) and net removal of one or more base cations, bicarbonate and silicate from solution. An example reaction is

$$\underset{\text{kaolinite}}{Al_2Si_2O_5(OH)_5} + 5\ Mg^{2+} + Si(OH)_4 + 10\ CO_3^{2-} + 5\ H_2O \rightarrow$$

$$\rightarrow \underset{\text{chlorite}}{Mg_5Al_2Si_3(OH)_8} + 10\ HCO_3^{-}$$

Important for salinity regulation in L. Chad (Carmouze, 1983), the quantative importance of 'reverse weathering' for an Ethiopian lake like L. Shala is uncertain. Yuretich & Cerling (1983) have adduced evidence that other forms of cation exchange by sediments, and solute burial in interstitial water, have been significant factors for reducing salinity increase in L. Turkana – where sediment input is large – during recent geological time.

In general, the time-variation of salinity can be viewed on the seasonal, historical, and geological time-scales. In Ethiopia the first is likely to be dominated by the alternation of wet and dry seasons. L. Abiata has received seasonal study by Wodajo & Belay (1984), who showed that in 1980–81 the conductivity varied between 19300 $\mu S\ cm^{-1}$ at the end of the rainy season and 22000 $\mu S\ cm^{-1}$ near the end of the dry. During recent years this relatively shallow lake has shown considerable fluctuations in its recorded salinity as evidenced by the different values in Tables 2 and 3 and the 50-year variation shown in Table 4. Some of this may spuriously derive from samples collected from the main access near the relatively dilute inflow. On a much larger scale, Lake Turkana shows a seasonal dilution towards the main R. Omo inflow after floodwater has entered (Hopson, 1982).

A number of analyses of Ethiopian waters date back to the Italian work of 1937 – 38; since then considerable changes in climate (especially rainfall) have occurred. A further example of significant climatic change is the appearance, in 1968, of L. Chelekleka (Teferra, 1980) in the vicinity of the Bishoftu crater lakes as a permanent water-body for the first time in living memory and its persistence to the present. Table 4 draws together some of the analyses carried out in the past 50 years. While any conclusions must be drawn with caution, open systems such as L. Tana, L. Zwei and L. Langano show little or no change whereas some more 'closed' lakes – including L. Awassa, L. Abaya and L. Chamo – have increased in salinity between the late 1930s and the mid-1950s by about 1.5 times. In the L. Abaya – L. Chamo pair, conductivity of the former (upstream) lake has averaged 790 μS cm^{-1} compared with the latter's approximately 1000 μS cm^{-1}. The relatively shallow L. Abiata which *in toto* drains a very large catchment seems more susceptible to changes in the balance between inflow and evaporation, and the lake showed a 2 to 3-fold increase of salinity between 1937 and 1961 and a significant dilution again by 1964. L. Shala, which is 20 – 30 times larger in volume than L. Abiata, did not show the same rise in salinity during 1937 to 1961, but nevertheless shows perceptible variation which may be part of a normal alternation between wet and dry seasons.

Salinity changes on the geological time-scale are beyond the present scope. They have received some attention for several now-closed lake basins, espe-

Table 4. The salinity (in g l^{-1}) of some Ethiopian lakes in recent years. All values are calculated (see Methods) except for references (1), (2), (3) and (9).

Year	1921	1926	1937 – 8	1961	1964	1966	1969	1970	1971	1976	1978	1980 – 1
Lake Ref.	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(6)	(11)
Garba Guratch								0.047		0.06		
Tana	0.168		0.151		0.143	0.147						
Zwei			0.354		0.349					0.312		
Hayq			0.580				0.770					
Awassa			0.650		1.008	0.995				0.861		
Abaya			0.517	0.90	0.908	0.819				0.768	0.72	
Chamo			0.651	1.063	1.112	0.907				0.953	1.00	
Langano			1.644	1.786	1.88	1.726			1.65	1.556		~1.6
Biete Mengest		1.94	1.538*		2.564							
Kilotes		6.76			5.73							
Abiata		8.13	8.358	19.38	16.20					12.96		~21
Shala			16.80	18.92	21.50				16.80	20.82		
Chitu						38.3			34.8			

(1) Grabham & Black (1925)
(2) Omer-Cooper (1930)
(3) Loffredo & Maldura (1941)
(4) Talling & Talling (1965)
(5) Original
(6) Belay & Wood (1982) for Abaya & Chamo, Talling (1976) for Tana, this paper for Awassa, Langano and Chitu.
(7) Baxter & Golobitsh (1971)
(8) Baxter & Golobitsh (1981)
(9) Baumann *et al.* (1975)
(10) Löffler (1978) for L. Garba Guratch, von Damm & Edmond (1984) for the others.
(11) Wodajo & Belay (1984)

* This value is probably in error as the authors give its k_{20} as 2335 μmho which suggests TDS approximately 2.5 g l^{-1}.

cially L. Turkana (reviews in Cerling, 1979, Beadle, 1981; Hopson, 1982), L. Abhe (Gasse, 1974b, 1975, 1977a; Gasse & Street 1978b; Gasse & Delibrias, 1976), L. Afrera (Gasse, 1974a; Gasse & Street, 1978b), and L. Shala (Grove *et al.*, 1975; Gasse & Street, 1978b).

Regularities of major ionic composition

Increasing salinity is accompanied by significant changes in the concentrations or proportions of all major ions. The latter conventionally comprise the anions Cl^-, HCO_3^- + CO_3^{2-}, and SO_4^{2-}, and the cations Na^+, K^+, Ca^{2+}, and Mg^{2+}. The ion sum HCO_3^- + CO_3^{2-} is here taken as equal to the measured alkalinity, neglecting proportionately small components of OH^- and $SiO(OH)_3^-$ in waters of high pH (>9.5). The locally abundant but less known F^- is also considered here. Some information on Li^+ concentrations (<0.1 meq l^{-1}) can be found in Baumann *et al.* (1975) and von Damm & Edmond (1984).

Chloride (Fig. 5a), as the most conservative anion, can be used as an index of evaporative concentration in East African waters (see later), and so its ratios with other constituents (Figs. 6, 9, 10) are of significance for interpretation. It shows a strong correlation ($r^2 = 0.89$) with conductivity over the whole series in Table 2 excluding L. Afrera and L. Assal. In the former – a saline lake of the Danakil depression – Cl^- is exceptionally the dominant anion, probably derived from past evaporites of seawater as is consistent with the isotopic evidence noted earlier. Chloride is also dominant in the still more saline L. Assal that receives seepage of sea-water. Near the other end of the salinity series, the concentration in L. Tana (44 μeq l^{-1}) is very low by general freshwater standards, as is that of its downstream derivative the Blue Nile by general river standards (Talling & Rzóska, 1967; Talling, 1976). From this can be deduced a low content of cyclic sea salt in the Plateau rainfall (cf. Table 5 from East African data) and of chloride leachable from the largely volcanic rocks of the drainage basin. These factors are also reflected in the low Cl^- concentration (<60 μeq l^{-1}) of the R. Omo (Table 3) and the R. Sobat Talling, 1976) derived from the Ethiopian highlands.

The chemically related but more interactive (and hence less conservative) fluoride (F^-) ion is known to reach high concentrations in many saline lakes of East Africa (Kilham & Hecky, 1973), where the rela-

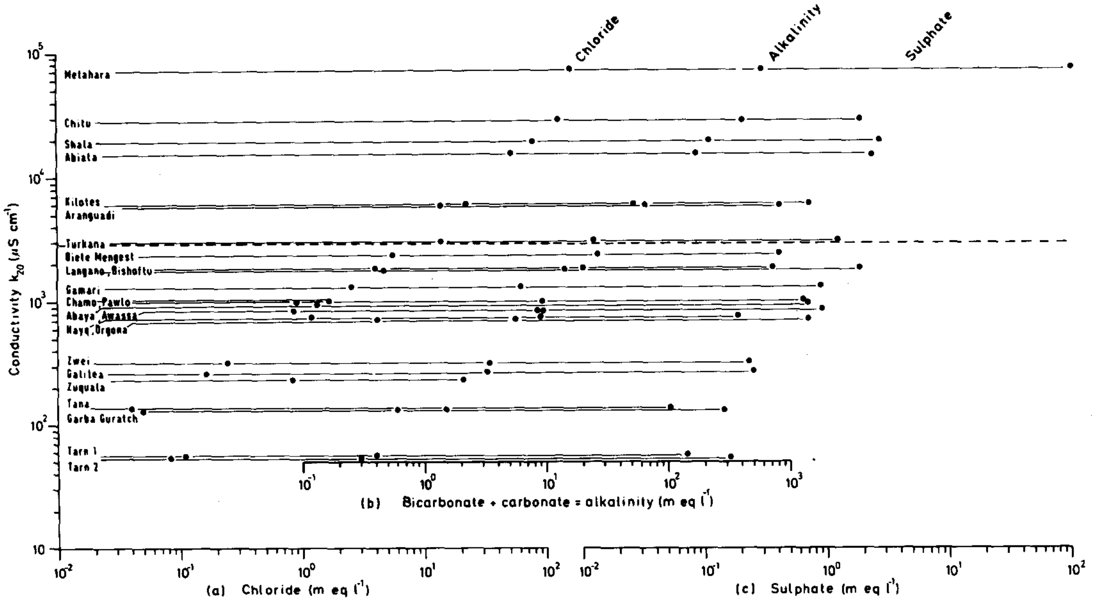

Fig. 5. Variation in concentrations of the principal anions (a) Cl^-, (b) alkalinity (bicarbonate + carbonate), and (c) SO_4^{2-} in surface waters from Ethiopian lakes arranged in order of electrical conductivity.

tionship with alkalinity – and hence salinity – appears often to be close (Cerling, 1979). This is broadly true for the north and south Rift lakes of Ethiopia, where F^- concentrations range from 0.081 meq l^{-1} in L. Zwei to 9.6–11.0 meq l^{-1} in L. Shala. The intermediate levels of 0.32–1.0 meq l^{-1} recorded from lakes Awassa, Langano, Abaya, Chamo and Turkana border the lower limit (0.5 meq l^{-1}) of concentrations known to have adverse effects on human bones and teeth. Although concentrations in most of the inflow rivers are less than 0.1 meq l^{-1} (von Damm & Edmond, 1984), Klein (1977) records values as high as 2.26 meq l^{-1} for fumarole waters feeding L. Abaya. In the much more saline L. Afrera of the Danakil depression concentrations are only 0.25–0.30 meq l^{-1} (Martini, 1969), compatible with marine influence.

Areas of marine transgression apart, even in the most dilute waters bicarbonate plus carbonate (alkalinity) are the dominant anion pair and a very high correlation with conductivity (r^2 = 0.94) results, with a mean ratio of conductivity 107 μS cm^{-1} per meq l^{-1} alkalinity (Fig. 5b). Nevertheless some alkalinity is proportionately lost as salinity increases; the alkalinity: chloride ratio falls to a fairly steady value of ~5 (by equivalents) when conductivity exceeds approximately 1000 μS cm^{-1} (Figs. 6a, 10), with a further marked decrease only in the very saline terminal L. Abhe. The relative loss of alkalinity is partially due to precipitation of calci-

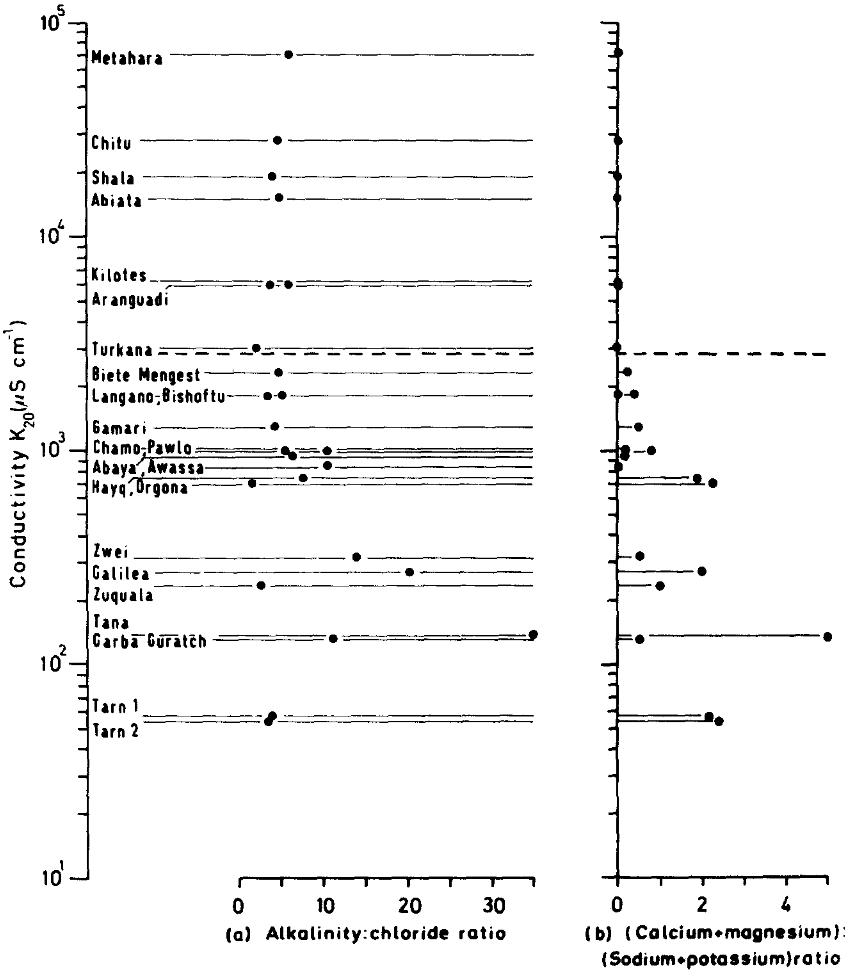

Fig. 6. The variation in (a) alkalinity: chloride ratios and (b) (calcium + magnesium) : (sodium + potassium) ratios in surface waters from Ethiopian lakes arranged in order of electrical conductivity.

um and possibly magnesium carbonates and Fig. 6b shows that the (Ca + Mg):(Na + K) ratio falls at the same point, conductivity 1000 μS cm^{-1}, in the salinity series. In addition von Damm & Edmond (1984) believed that over half of the lost alkalinity could be due to 'reverse weathering', the formation of alumino-silicate minerals such as smectite. Baumann *et al.* (1975) found smectite in abundance in the sediments of L. Shala but report it as poorly crystallised, which suggests it might be weathered input rather than material produced by reverse weathering.

The upward trend in pH which acompanies increasing alkalinity is shown in Fig. 7. The results presented are field values rather than air-equilibrium values (depicted for various African lakes, some Ethiopian, by Talling & Talling, 1965), and where repeated measurements are available their range and divergence from air-equilibrium values reflect the CO_2-metabolism of the lakes. This is particularly

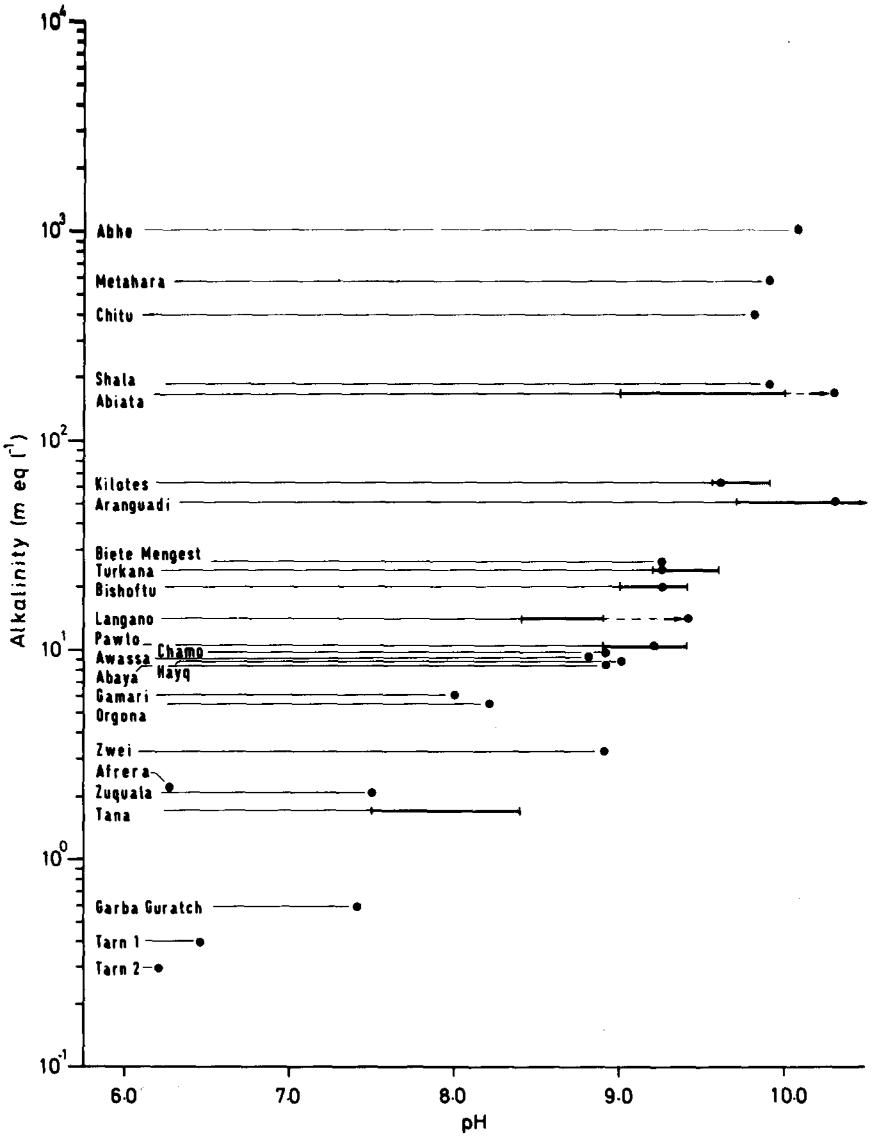

Fig. 7. The variation in pH with alkalinity in surface waters from Ethiopian lakes. Horizontal bars represent ranges of pH measured in the field.

noteworthy in lakes such as L. Aranguadi where, in spite of buffering by bicarbonate + carbonate alkalinity in excess of 50 meq l^{-1}, dense phytoplankton crops and vigorous photosynthesis and respiration can shift pH upwards through more than one pH unit (Talling *et al.*, 1973). The positive linkage of pH with alkalinity rather than salinity is illustrated by its divergent values in lakes Abhe and Afrera, which are of similar high salinity but of very different alkalinity (Table 2).

Sulphate (Fig. 5c) in general contributes the smallest fraction of the major anions. This feature, common in East and Central Africa, can primarily be related to a low denudatory contribution from rocks containing little sulphate. The correlation with conductivity is also lower, which reflects both the variable but generally low values of sulphate in inflows (even hot-spring water in Ethiopia has rarely been observed as 'sulphurous') and the reduction of sulphate to sulphide in the anoxic hypolimnia of productive lakes. For example Wood *et al.* (1984) have shown that most (probably at least 70%) of the total sulphate + sulphide−S in L. Pawlo was at times in the reduced form. Additionally, sulphide is reported by Baumann *et al.* (1975) from the deep chemical stratification of L. Shala, with sulphate reduced to undetectable levels in the interstitial water of the sediments. According to the analyses of Baumann *et al.* and von Damm & Edmond (1984), the surface water of this lake has a distinctively low proportion of sulphate, but in our own analyses (by an ion-exchange rather than turbidiometric method) the proportion is much higher. Reduction of sulphate followed by loss of sulphide to atmosphere (as H_2S) or sediments (as S^{2-}) will yield an increment of alkalinity (Kilham, 1984). Loss of sulphate as gypsum ($CaSO_4 \cdot 2H_2O$) is prevented in most Ethiopian and East African waters by low levels of Ca^{2+}, but is recorded in sediments of the marine-influenced L. Assal and L. Afrera (Gasse & Street, 1978b).

Among cations (Fig. 8) sodium is moderately conservative and shows close correlation ($r^2 = 0.94$) with conductivity. As far along the series as L. Orgona (conductivity 700 μS cm^{-1}) sodium may be present in lower concentration than calcium, but in waters above approximately 1000 μS cm^{-1} sodium is the ever-increasing dominant. Potassium also increases throughout the series (Fig. 8b) though the correlation with conductivity is much poorer, presumably due to interactions with sediment minerals involving ion-exchange and precipitation of potassium-rich silicates.

Quite different trends are shown by the bivalent cations calcium and magnesium (Fig. 8c, d). In relative proportion Ca^{2+} is the dominant cation in several waters of low salinity, including L. Tana and

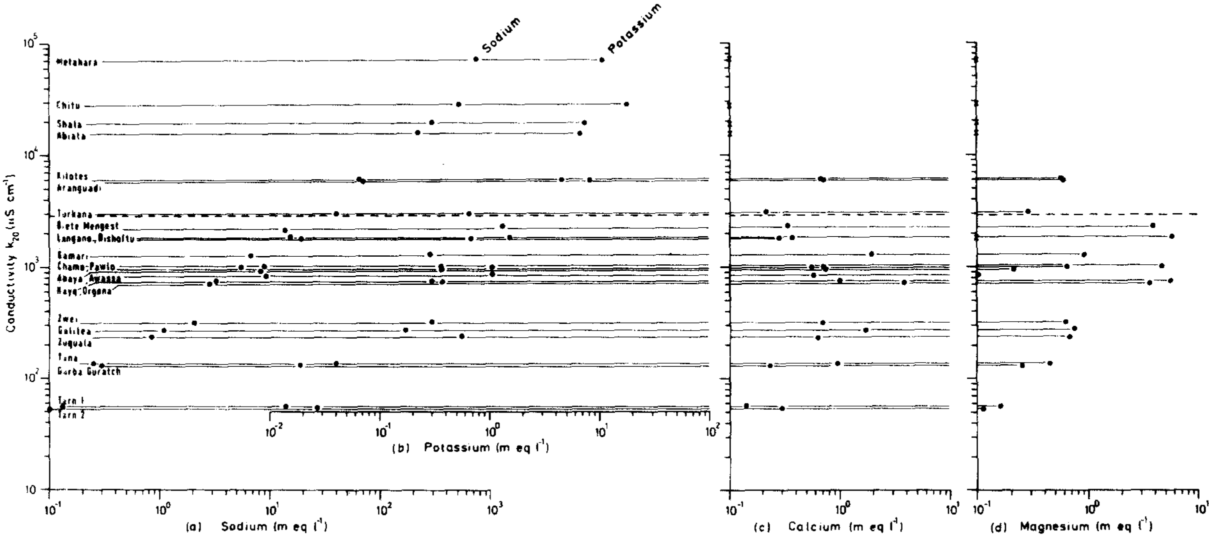

Fig. 8. The variation in concentration of the principal cations (a) Na^+, (b) K^+, (c) Ca^{2+} and (d) Mg^{2+} in surface waters from Ethiopian lakes arranged in order of electrical conductivity. In (c) and (d) X represents values below the limits of detection.

the Blue Nile which traverses a gorge with thick beds of limestone. As in many other African lakes (Talling & Talling, 1965; Cerling, 1979) a progressive increase of their concentrations with salinity is precluded by the precipitation of relatively insoluble carbonates from CO_3^{2-} rich waters of high alkalinity and, for K^+, by ion-exchange with sediment minerals. The situation is different in L. Afrera and L. Assal where the brine more resembles sea water. In general, however, calcium reaches maximum concentrations around the 1000 μS cm^{-1} index of salinity and magnesium between 1000 and 2000 μS cm^{-1}. Magnesium is often strongly preponderant over calcium in the intermediate conductivity range 1000–2400 μS cm^{-1}, especially in the Bishoftu lakes Pawlo, Bishoftu, and Biet Mengest. Its later elimination with rising salinity is distinctive of bicarbonate – carbonate waters and not of a salinity series where this component is in generally lower (0.2–0.45) fractional anionic representation (Golterman & Kouwe, 1980). Two exceptions to the tendency for both calcium and magnesium to fall to very low concentrations at high alkalinity – a feature quantitatively modelled by Cerling (1979) – are shown by L. Aranguadi and L. Kilotes, both with conductivity 6000 μS cm^{-1}. Rippey & Wood (in press) have argued that very high concentrations of soluble phosphorus described below are probably responsible for the calcium carbonate supersaturation first reported by Prosser *et al.* (1968). Although L. Chitu is rather similar to L. Aranguadi (not least because its phytoplankton is strongly dominated by*Spirulina platensis*) with very high phosphate concentrations, its overall salinity is 4–5 times that of L. Aranguadi and presumably any stabilising effect of soluble phosphorus is overridden.

Processes of exchange or precipitation of cations can initiate some chemical stratification with depth in many lakes elsewhere. Baxter *et al.* (1965) showed that in L. Pawlo, during a period of strongly developed stratification, calcium increased from 0.46 meq l^{-1} at the surface to 0.90 meq l^{-1} at 55 m and that this was balanced by an increase in HCO_3^- + CO_3^{2-} alkalinity from 10.08 to 10.55 meq l^{-1}. A combination of lower pH and higher soluble phosphorus concentration at depth, and possible sedimentation of precipitated $CaCO_3$ from above, provide a plausible explanation of the observation. Magnesium (at 4.81 ± 0.06 meq l^{-1}) did not show such differences in vertical distribution. Although calcium and alkalinity were not routinely determined in the subsequent lengthy study of thermal and chemical stratification (Wood *et al.*, 1976, 1984), prolonged and large differences in the vertical distribution of pH and phosphate suggest that differential Ca^{2+} accumulation and persistance at depth could be an important process in moderately saline lakes near the limit of calcium carbonate solubility. In contrast, for the more saline L. Turkana, Harbott (in Hopson, 1982) reports a slight fall in calcium concentration from 25 to 100 m depth and a disproportionately larger fall in alkalinity. Geochemical processes in this lake involving cations have been examined by Yuretich & Cerling (1983). Their results show that Ca^{2+} is precipitated as calcite, and Na^+ and Mg^{2+} are removed by ion-exchange processes. Small increases in salinity and major ions with depth are recorded in the saline L. Shala (Baumann *et al.*, 1975, von Damm & Edmond, 1984) and a large increase in L. Assal (Brisou *et al.*, 1974). In the Cl^--rich L. Afrera, Gonfiantini *et al.* (1983) found no significant layering of major ions, but some of ^{18}O and deuterium proportions, across a deep temperature gradient.

Quantitative aspects of evaporative concentration

In any series with evaporative concentration, the interpretation of ionic composition may consider that of parent atmospheric precipitation and the more conservative status – relative to secondary changes – of some components. Chemical analyses of atmospheric precipitation are apparently not available for Ethiopia, but two published and partly overlapping series do exist from largely inland sites in neighbouring East Africa (Rodhe *et al.*, 1981, Gaudet & Melack, 1981). Their mean or median concentrations of components are similar, and averages of these are used here (Table 5). Comparing with the ionic proportions in seawater, and assuming that the Cl^- content is of marine origin, it can be deduced (Table 5) that interaction with dust (a form of chemical denudation) is responsible for a large (× c. 25)

Table 5. Concentrations (in μeq l^{-1}) of major ions in East African atmospheric precipitation (i – iii) and five Ethiopian surface waters of low salinity, with concentrations and proportional contributions of non-marine and surface denudative components distinguished. It is assumed that all Cl^- is of cyclic marine origin and that the values (ii) for atmospheric precipitation are representative.

		Cl^-	Na^+	K^+	Ca^{2+}	Mg^{2+}	SO_4^{2-}	$HCO_3^- + CO_3^{2-}$
(i)	atmospheric precipitation							
	Gaudet & Melack (1981) (mean)	12	23	8	9	19	15	20
	Rodhe *et al.* (1981) (median)	17	27	8	19	7	16	24
(ii)	mean of above	15	25	8	14	13	15	22
(iii)	marine contribution in (ii)							
	as concn	[15]	13	0.3	0.6	3	1.5	0.06
	as fraction	[1.00]	0.52	0.03	0.04	0.22	0.10	0.003
(iv)	Tarn 2 (Bale Mts) lake water, concn	84	100	27	300	110	160	300
	marine component, concn	[84]	72	1.5	3.1	16	8.4	0.4
	evapo-concn factor to (ii)	5.6						
	non-marine component,							
	as concn	[0]	28	25.5	297	94	152	300
	as fraction	[0]	0.28	0.94	0.99	0.85	0.95	>0.99
	surface-denudative component,							
	as concn	[0]	−40	−18	222	37	76	177
	as fraction	[0]	−0.40	−0.66	0.74	0.34	0.47	0.59
(v)	L. Tana							
	lake water, concn	44	240	40	945	450	52	1520
	marine component, concn	[44]	38	0.8	1.6	8.6	4.4	0.2
	evapo-concn factor to (ii)	2.9						
	non-marine component,							
	as concn	[0]	202	39	943	441	48	1520
	as fraction	[0]	0.84	0.98	>0.99	0.98	0.92	>0.99
	surface-denudative component,							
	as concn	[0]	167	17	904	412	8.5	1456
	as fraction	[0]	0.70	0.42	0.96	0.92	0.16	0.96
(vi)	L. Galilea							
	lake water	160	1060	170	1700	72	240	3220
	marine component, concn	[160]	138	2.9	5.9	31	16	0.7
	evapo-concn factor to (ii)	11						
	non-marine component,							
	as concn	[0]	922	167	1694	41	224	3219
	as fraction	[0]	0.87	0.98	>0.99	0.57	0.93	>0.99
	surface-denudative component,							
	as concn	[0]	785	82	1546	577	75	2978
	as fraction	[0]	0.74	0.48	0.91	0.80	0.31	0.92
(vii)	L. Zwei							
	lake water, concn	240	2110	300	700	615	220	3340
	marine component, concn	[240]	206	4.3	8.9	47	24	1.0
	evapo-concn factor to (ii)	16						
	non-marine component,							
	as concn	[0]	1904	296	691	568	196	3339
	as fraction	[0]	0.90	0.99	0.99	0.92	0.89	>0.99
	surface-denudative component,							
	as concn	[0]	1710	172	476	407	−20	2988
	as fraction	[0]	0.81	0.57	0.68	0.66	−0.09	0.89

Table 5. Continued.

		Cl^-	Na^+	K^+	Ca^{2+}	Mg^{2+}	SO_4^{2-}	$HCO_3^- + CO_3^{2-}$
(viii)	headwater stream of R. Awash							
	stream water, concn	230	690	130	1710	1000	-	3160
	marine component, concn	[230]	198	4.1	8.5	45	-	1.0
	evapo-concn factor to (ii)	15						
	non-marine component,							
	as concn	[0]	492	126	1701	955	-	3159
	as fraction	[0]	0.71	0.97	>0.99	0.95	-	>0.99
	surface-denudative component,							
	as concn	[0]	315	10	1500	805	-	2830
	as fraction	[0]	0.46	0.08	0.88	0.80	-	0.90

relative enhancement of Ca^{2+} and K^+ and lesser ones of Na^+, Mg^{2+}, and SO_4^{2-}. It may influence the large HCO_3^- -alkalinity enhancement which mainly depends upon relationships with atmospheric CO_2 and H^+.

The transition from rainwater to the least saline Ethiopian lake waters involves ionically-selective chemical weathering and unselective evaporative concentration. If it is assumed that the former source of Cl^- is negligible (as by Gaudet & Melack, 1981 for a Kenyan lake), and that Cl^- is a chemically conservative component, ratios of Cl^- concentration will be estimates of evaporative concentration factors. In this three transitions may be considered: from (i) atmospheric precipitation to surface run-off, (ii) surface run-off to open-lake water, and (iii) surface run off to closed-lake water. All are represented in a continous scale of Cl^- concentration (Figs. 9, 10). Example factors for transition (i) and (i) + (ii) are calculated in Table 5, and are least (2.9 – 5.6) for high altitude tarns and L. Tana in regions of higher rainfall and humidity. In the lower rainfall region of the north Rift (Galla lakes) and near Addis Ababa, Cl^- concentration in river waters is often 0.15 – 0.3 meq l^{-1} (Table 3; von Damm & Edmond, 1984) and so indicative of a transition (i) factor of 10 – 20. A low value of ~ 2 applies to the transition (ii) factor for L. Zwei (von Damm & Edmond, 1984), a lake of low retention time (Makin *et al.*, 1976), and one of ~ 3 (miscalculated as 1.2 by von Damm & Edmond, 1984) for L. Abaya where the inflows show evidence of more evaporative concentration, involving ground water. For an open lake of longer retention, Langano, the transition (ii) factor is higher (c. 20 – 40), although the very high value of 69 for Langano shown by von Damm & Edmond (1984) appears from our analyses (Table 3) to be an overestimate. An island hot spring (not analyzed by von Damm & Edmond) provides input from saline ground water rich in Cl^-, which may account for usually high ratios of Cl^- to alkalinity and salinity in this lake. The closed terminal lakes of Abiata, Shala, and Turkana have high transition (iii) factors of about 100, 300, and 93 respectively, reflecting the historical dimension (also expressed by *accumulation* or *response time* = Cl^-stock/Cl influx rate: e.g. Yuretich & Cerling, 1983; von Damm & Edmond, 1984) rather than local evaporative rates. A greater incidence of reflux pathways, as hot saline springs, is probably also of significance. Such springs as Sodere ($[Cl^-]$ = 5.0 meq l^{-1}, alkalinity 23 meq l^{-1}, $[SiO_2]$ 130 mg l^{-1}) and possibly elsewhere must alter the composition of the R. Awash considerably from surface run-off. However its water shows a transition (ii) factor at the open L. Gamari of only 1.7, and a transition (iii) factor at the terminal L. Abhe of 700. For the saline lakes Afrera and Abiata there is strong isotopic evidence of past evaporation (Gonfiantini *et al.*, 1973; Craig, 1977 quoted in von Damm & Edmond, 1984).

The maximal evaporative concentration factor relative to precipitation for the large low-salinity lakes Tana and Zwei is 2.9 and 16 respectively, values too low to account for more than a small fraction

(< 1/3) of the concentrations of Ca^{2+}, Mg^{2+}, Na^+, and HCO_3^- in these lakes, which must therefore depend mainly on surface chemical denudation (Table 5). The same conclusion applies to a headwater stream, and L. Galilea, a reservoir on the Awash River, which more closely approach surface run-off. In absolute terms, the largest denudative inputs are of Ca^{2+}, Na^+, Mg^{2+} and HCO_3^-, to which Si (as $Si(OH)_4$ and $SiO(OH)_3^-$, although here expressed as SiO_2) must be added. Sources of Ca^{2+} and HCO_3^- in parent sedimentary rocks and volcanic carbonatites have already been mentioned. Indirect generation of HCO_3^- can result from the weathering of alumino-silicates, and there is likely to be a ready availability of Si at c. 1 $mmol^{-1}$ levels from porous volcanic rocks (Gaudet & Melack, 1981; von Damm & Edmond, 1984).

If further advance up the Ethiopian salinity series (e.g. >500 $\mu S\ cm^{-1}$) were due only to chemically-unselective evaporative concentration, concentrations of major constituents would bear near-constant proportions to each other. In reality deviations occur, similar to those described for African lake waters by Talling & Talling (1965) and further analyzed and schematized by Eugster (1970), Cerling (1979), and Eugster & Jones (1979), that are indicative of other physical and chemical pathways. Some but not all of these are reproducible in evaporation experiments, as carried out by Gac and co-workers (Gac, Droubi, Fritz & Tardy, 1977; Gac, 1980) on water from L. Chad and its inflow. The pathways (Cerling, 1979) include the precipitation of calcite, and – at very high salinities – natron and trona; the depletion of Mg^{2+} by precipitation as carbonate or by the conversion of Si-Al detritus and kaolinite to montmorillonite; of K^+ by clay-interaction; of Na^+ by sediment ion-exchange; of SO_4^{2+} by bacterial reduction; and of HCO_3^- and $Si(OH)_4$ by 'reverse weathering' of sediment minerals. In these processes Cl^- is generally conservative and – as noted above – the best measure of evaporative concentration, unless exceptionally a separate influence of marine brines exists (L. Assal, L. Afrera). In the higher salinity lakes the determining ion activities fall well below their concentrations, especially for bivalent ions, as illustrated for Ca^{2+} and Mg^{2+} by Cerling (1979).

When plotted against Cl^- concentrations (Figs. 9, 10), concentrations of the six other major ionic components show three main types of behaviour. These can be interpreted by comparison with diagonal lines that represent simple evaporative concentration of the component levels and proportions found in atmospheric precipitation (P). Such a line for Na^+ is inserted in Figs. 9 and 10. For waters closer to surface run-off and with limited evaporative concentration from P (factor <100), surface chemical denudation produces an upward displacement of points that is especially marked for the ions Ca^{2+}, Mg^{2+}, Na^+, and HCO_3^-. This denudative component is estimated in Table 5 as both absolute and relative contributions to major ions in five waters of low salinity, as the difference between actual concentrations and those expected from a combination of concentrations in mean atmospheric precipitation and the Cl^--based concentration factor. Unlike the analogous calculation introduced by Dunne (1979), the present estimates omit the chemical denudation already represented in

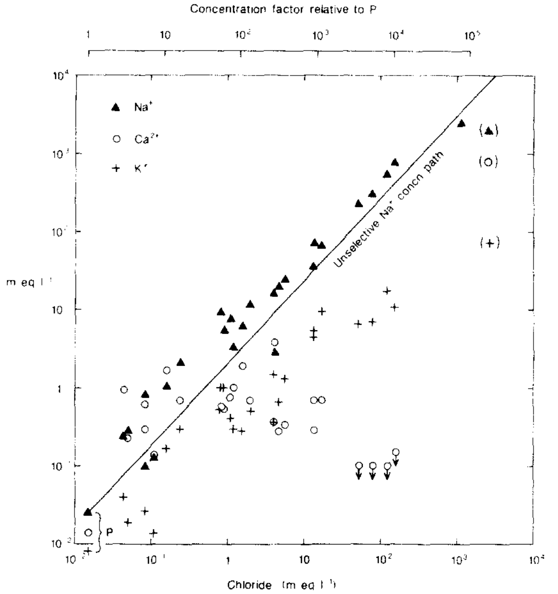

Fig. 9. Variation in Ethiopian lake waters of the concentrations of Na^+, Ca^{2+}, and SO_4^{2-} in relation to Cl^- concentration, with (above) a scale of evaporative concentration relative to mean atmospheric precipitation (P). A diagonal line represents passive concentration of Na^+ from its value in atmospheric precipitation. Arrows indicate concentrations below the levels of detection shown. ( ) enclose points for L. Afrera with other marine influence.

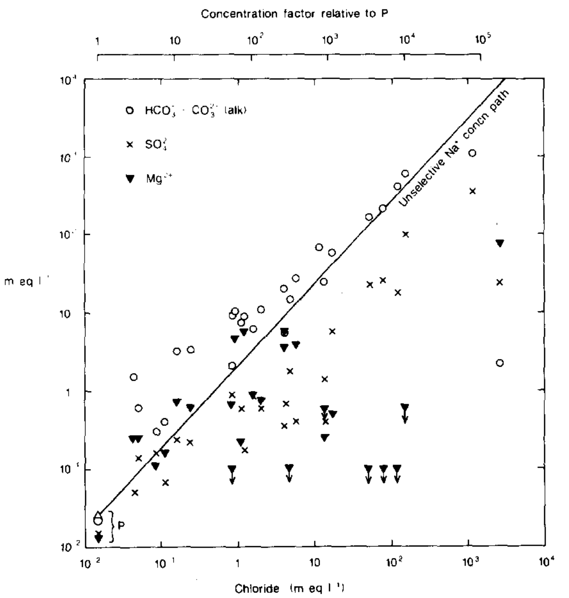

Fig. 10. Variation in Ethiopian lake waters of the concentrations of $HCO_3^- + CO_3^{2-}$ (alkalinity), Mg^{2+}, and K^+ in relation to Cl^- concentration. Other features as in Fig. 9.

atmospheric precipitation. At higher concentration factors non-denudative modifications occur within the lake basins, that are expressed in (i) a less than proportional increase in Na^+ and HCO_3^-, (ii) elimination of Ca^{2+} and Mg^{2+}, and (iii) a wide scatter in K^+ and SO_4^{2-} superimposed on an upward, less than proportionate, trend. These trends are also recognisable in the log [ion]/log[Cl^-] plots of Eugster & Jones (1979), Kilham (1984), and von Damm & Edmond (1984) based on East African or Ethiopian lakes, and (ii) and (iii) in plots against components whose variation is strongly correlated with that of Cl^- (e.g. alkalinity: Cerling, 1979; Na^+: Eugster, 1970).

To these correlated components may be added salinity and conductivity, the basis of the earlier seriation of Ethiopian waters although conductivity is quantitatively imperfect by its depression at high ionic strength. As the dominant cation, Na^+ bears a ratio to salinity that is inherently stable in this salinity region. The corresponding ratio for the dominant anion-pair, $HCO_3^- + CO_3^{2-}$, is probably only appreciably modified at high salinity by internal carbonate precipitation or marine inputs, when the proportion of Cl^- increases. Besides the examples of lakes Assal and Afrera, a high Cl^- concentration is recorded by Grove *et al.* (1975) during an ephermeral reflooding of the dried lake bed of Chew Bahir ([Cl^-] = 4110 mg of 116 meq l^{-1}), probably in excess of the alkalinity for which the record is ambiguous. Although the terminal L. Abhe is an example, there is no widespread occurrence in Ethiopia of the higher-chloride subcategory of sodium bicarbonate-dominated lake waters distinguished by Kilham (Kilham & Hecky, 1973; Hecky & Kilham, 1973) in East Africa, and ascribed to stronger evaporative concentration of a Cl^--rich precursor under more arid climates.

Major plant nutrients

Concentrations of soluble and largely inorganic forms of the elements silicon, phosphorus and nitrogen are surveyed below. All are liable to time-changes by biological uptake and release, which have been followed only for the Bishoftu group of crater lakes (Wood *et al.*, 1984).

(a) Silicate

The 20 lakes for which silicate data – expressed as SiO_2 – are available (Table 2) show a variable but broadly upward trend of concentration with increasing salinity (Fig. 11). Most concentrations are very high by world standards. Contributory factors are the greater mobility of silicate in most tropical soils and porous volcanic lavas, the importance of ground-water input for many lakes, and the enhanced dissolution of solid silicates in saline waters of high alkalinity and pH.

The presence or absence of diatoms as major contributors to the flora may markedly influence the variation of silicate in surface waters and, as shown later, there is some evidence that diatoms play a quantitatively more important role as phytoplankters in the less saline waters. Baxter & Golobitsh (1971) showed a four-fold increase in silicate concentration at 70 m depth compared with surface water in L. Hayq, where diatoms were believed to be a major constituent of a sparse algal biomass, and

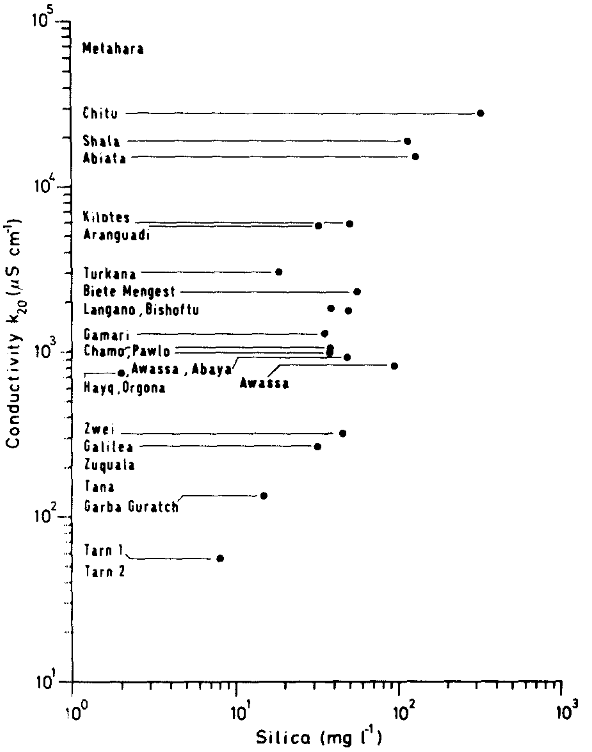

Fig. 11. The variation in concentration of soluble reactive silicate (expressed as silica) in surface waters from Ethiopian lakes arranged in order of electrical conductivity.

also a fall from 20 mg SiO_2 l^{-1} in the inflowing Ancherca R. to 1 mg l^{-1} in the surface waters of the lake. In L. Pawlo, a closed yet not very saline crater lake fed by groundwater where diatoms play a very minor role in the phytoplankton, a representative concentration at the surface is 77 mg SiO_2 l^{-1} rising to 96 l^{-1} in the hypolimnion (Wood *et al.*, 1984). Silicate will also be removed from solution in the 'reverse weathering' process of sediment formation (p. 42).

(b) Phosphate

Although there is a broad trend of increasing soluble reactive phosphate concentration with increasing salinity (Fig. 12), the relationship is still less regular than that for silicate. Among the possible sources of irregularity (p. 52), abiogenic and biogenic transformations in the lakes are likely to be important. Thus if either of the approximate order-of-magnitude ratios of phosphorus to chlorophyll *a* in phytoplankton adopted by Talling (1981) are applied to the present data, direct algal incorporation is generally appreciable in relation to residual soluble reactive phosphorus. Only when the latter reaches several milligrams per litre, as in L. Aranguadi, are the upper limits to phytoplankton production (Talling *et al.*, 1973) likely to lessen the proportion of phosphorus in direct algal combination. Direct measures of algal incorporation of phosphorus are available from a productive soda lake in Kenya, L. Nakuru, for which 1972–3 concentrations of total P were 9850 ± 1100 μg l^{-1}, filtrate P 3890 ± 1560 μg l^{-1}, and soluble reactive P 149 ± 53 μg l^{-1} (Vareschi, 1982).

A more regular trend with salinity cleared of some of the seasonal variation in biomass might result from considering total P, but even this could be disturbed by the effects of rivers in spate discharging high concentrations of particulates in the rainy season. Most of the few available values of total P (9 Ethiopian lakes) are listed by Talling & Talling (1965), who illustrate a positive relationship with salinity.

Phosphate has been determined more often in some lakes, permitting ranges of values for surface waters to be illustrated (Fig. 12). A less saline lake such as L. Chamo shows a range covering nearly 300 μ l^{-1} PO_4-P and the highly productive L. Araguadi a range of some 1500 μg l^{-1}. The large range in the productive L. Abaya, with abundant plankton dominated by *Microcystis aeruginosa*, is also notable. It is quite likely that detailed studies would show many lakes to behave similarly, given the variation in biomass measured (inserted where available on Fig. 12 as chlorophyll *a* concentrations) and recognising the very considerable effect which prolonged thermal stratification may have on the vertical distribution of soluble phosphate and on sediment/water equilibria in Ethiopian lakes (Prosser *et al.*, 1968; Wood *et al.*, 1984).

(c) Nitrogen

The uncertainties of transformation which surround

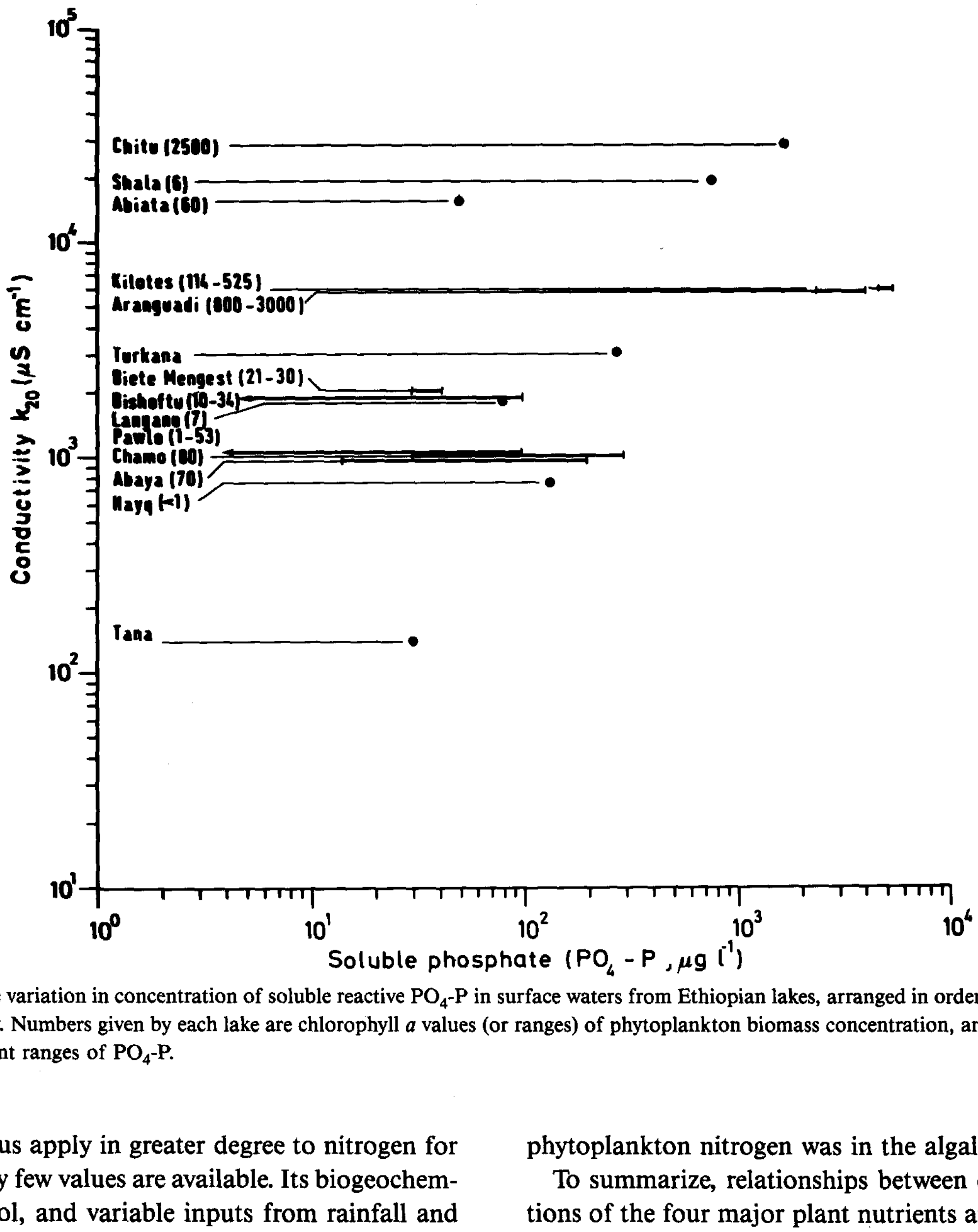

Fig. 12. The variation in concentration of soluble reactive PO_4-P in surface waters from Ethiopian lakes, arranged in order of electrical conductivity. Numbers given by each lake are chlorophyll *a* values (or ranges) of phytoplankton biomass concentration, and horizontal bars represent ranges of PO_4-P.

phosphorus apply in greater degree to nitrogen for which very few values are available. Its biogeochemical control, and variable inputs from rainfall and nitrogen-fixation, make an overall evaporative concentration and relationship with salinity improbable. In the Bishoftu crater lakes, where the depth-time distribution of inorganic (largely NO_3^- and NH_4^+) nitrogen has been determined over several years (Wood *et al.*, 1984), it was observed that nitrate was seldom detectable in surface waters, and then only after recent stirring to the surface and oxidation of ammonia which, on a water-column basis, represented 90 to 100% of the total inorganic nitrogen. Further, in the extremely productive L. Aranguadi, at times over 90% of the total inorganic + phytoplankton nitrogen was in the algal biomass.

To summarize, relationships between concentrations of the four major plant nutrients and salinity range between strongly positive (total inorganic C), moderately positive (P), weakly positive (Si), and probably non-existent (N). Of these, quantities of C and P are respectively strongly or more weakly conserved during evaporative concentration, and those of Si are often considerable in run-off but also promoted by alkaline dissolution of their universal mineral precursors. Variation also occurs from widespread biological transformations, which relative to stocks appear generally small for total inorganic C and Si, larger for P, and probably predominant for N.

Heavy metals

The total iron content is unusually high, for surface oxygenated water, in a number of Ethiopian rift lakes – where the lake water is visibly discoloured. Concentrations in lakes Zwei (5000 μg l^{-1}), Langano (9400), Abaya (13500) and Shala (13000) can be cited from the 1961 samples of Talling & Talling (1965), contrasting with lower and more 'usual' concentrations in lakes Abiata (440) and Metahara (500). There is no obvious relation with salinity, nor with algal production.

The few analyses for other metals do not show exceptionally high concentrations in lake waters. Concentrations of Cu, Zn, and Pb are recorded by Baumann *et al.* (1975) for lakes Langano, Abiata, Shala and Chitu; none exceed 40 μg l^{-1}. Those of Co, Ni, Ag and Cd were less than 3 μg l^{-1}. Concentrations of all these metals were also low in thermal inputs to these rift lakes, which thus differ from the deep thermal sources in the Red Sea. The study of L. Abaya by Klein (1977) was primarily concerned with heavy metals and their possible involvement in non-parasitic elephantiasis. He reports analyses of the lake waters as follows: Hg (2 and 30 μg l^{-1}), Pb (2 to 3 μg l^{-1}), Cr (17 and 47 μg l^{-1}, As (0.1 and 0.25 mg l^{-1}) and B (0.2 and 0.5 mg l^{-1}). The fumarole water contained 850 μg Hg l^{-1} and 1.0 mg As l^{-1}. Zn, Cu, Cd, Ba and Ag were not detected.

Phytoplankton

Any attempt to relate the algal flora to salinity must be made with extreme caution. Most collections of plankton have been from expeditions or short visits, identification beyond genus level is often lacking and there is very little knowledge of seasonal aspects of floristic changes. Even where long-term studies have been carried out, on the Bishoftu crater lakes, and the almost continuous dominance of a single or at most two species was established, detailed counts of other species were not made. As with many lakes in the world, information on smaller nannoplankton ($<5-10$ μm) is virtually absent. Recognition must also be made of taxonomic uncertainties, synonymy and nomenclatural changes (see also footnote to Table 6). Thus it is probable that the entity widely recorded as the halophile *Spirulina platensis* (Nordstedt) Geitler (other synonyms *Arthrospira platensis* (Nordstedt) Gom., *Oscillatoria platensis* (Gom.) Bourrelly, *Spirulina geitleri* De Toni, *Spirulina maxima* (Setchell et Gardner) Geitler) is more correctly *S. fusiformis* Voronichin (Hindák, 1985); *Microcystis flos-aquae* can be regarded as a form of *M. aeruginosa* Kütz. (Komárek, 1958); the dominant *Melosira* sp. of L. Tana has been variously recorded as *M. granulata* var. *jonensis* f. *procera* Grun. (Talling & Rzóska, 1967) or *M. italica* (Ehr.) Kütz. var. *bacilligera* O. Müller (Gasse, 1975, 1986; Gasse *et al.*, 1983). For blue-green algae it is possible that a conclusion of Komárek (1985), based upon the Cuban flora, may apply more generally in the tropics – that >40% of species cannot be reliably identified from existing taxonomic information.

Table 6 summarizes available data on the phytoplankton reported from 19 Ethiopian lakes. For diatoms alone Zanon (1942), Gasse *et al.* (1983), and Gasse (1986b) give more detailed information.

Table 6. The species composition of phytoplankton* recorded at various times (1937 – 1980) in Ethiopian lakes of given conductivity and alkalinity.

Lake	Date	Reference	Conductivity k_{20} (μS cm^{-1})	Alkalinity (meq l^{-1})	Dominant algae	Other common forms
Tana	1937	(1) (2)	–	1.70	Surirella spp., Synedra spp., Melosira spp., Anabaena spp.	Pediastrum clathratum, Staurastrum leptocladum, Closterium spp., Eudorina elegans
	Mar. '64	(3) (4) (5)	137	1.52	Melosira granulata var. jonensis f. procera and/ or M. italica, Anabaena sp.	Staurastrum spp., Pediastrum clathratum, Mallomonas sp., Surirella sp.

Table 6. Continued.

Lake	Date	Reference	Conductivity k_{20} (μS cm^{-1})	Alkalinity (meq l^{-1})	Dominant algae	Other common forms
	Nov. '71	(6)	-	-	Melosira italica var. bacilligera, M. agassizii, M. italica	Melosira italica var. tenuissima M. distans, Surirella biseriata, S. muelleri, Stephanodiscus astraea, S. hantzschii
Galilea	Mar. '64	(3)	274	3.22	Euglena sp., Trachelomonas sp., Melosira granulata var. angustissima f. spiralis	Mallomonas sp., Closterium sp., Gonium sp., Raphidiopsis sp., Peridinium sp., μ-flagellates
Zwei	1937–8	(7)	372–427 (8)	-	Aphanothece microspora, Chroococcus dispersus, Gloeotrichia echinulata	Microcystis flos-aquae, Spirulina sp., Pediastrum boryanum, P. integrum, P. duplex, Merismopedia tenuissima, Coelastrum sp., Kirchneriella obesa, Scenedesmus quadricauda, Staurastrum sp., Euastrum sp., Surirella ovalis
	May '61	(3)	370 (9)	3.92 (9)	Spirulina spp., Lyngbya spp.	Aphanothece sp., Aphanocapsa sp.
	Mar. '64	(3)	322	3.34	Oscillatoria spp.	
Hayq	1938	(7)	837 (8)	-	Microcystis flos-aquae, M. aeruginosa, Phormidium sp., Peridinium sp.	Surirella ovalis, Pediastrum boryanum "many forms"
	1941	(10)	-	-	Amphora ovalis libyca, Epithemia argus, E. sorex, E. turgida, Gomphonema sp., Synedra ulna, Rhoicosphenia curvata, Surirella biseriata, S. tenera var. nervosa	Nitzschia navicularis, N. virgata, Gyrosigma fasciola
	Jan. '69	(11)	750	9.1	Botryococcus sp.	Epithemia sp., Rhoicosphenia sp., Spirogyra sp.
Awassa	1938	(7)	790–860 (8)	-	Pediastrum simplex, P. integrum, P. duplex, Selenastrum gracile, Scenedesmus quadricauda, S. obliquus	Microcystis flos-aquae, Aphanothece microspora, Merismopedia tenuissima, Spirulina sp., Euastrum sp., Melosira italica, Synedra tubulata, Surirella linearis, Anomoeneis sphaerophora
	May '61	(3) (12)	1050 (9)	10.5 (9)	Aphanothece spp., Spirulina spp., Aphanocapsa spp.	Merismopedia sp., Cryptomonas sp., Surirella sp.
	Feb./Mar. '64		830	9.20		
Abaya	1937	(7) (13)	680 (7)	-	Microcystis flos-aquae	Pediastrum simplex (rare)
	May '61	(3)	900 (9)	8.50 (9)	Microcystis aeruginosa	Synedra sp., Botryococcus braunii, Gomphosphaeria lacustris
	Feb. '64	(3)	623	7.41		
Chamo	1937	(7)			Microcystis flos-aquae	Gomphosphaeria lacustris, Peridinium sp. (rare), Pediastrum simplex, Anabaenopsis circularis
	Feb. '64	(3)	1100	10.9	Aphanocapsa sp., Microcystis sp.	

Table 6. Continued.

Lake	Date	Reference	Conductivity k_{20} (μS cm^{-1})	Alkalinity (meq l^{-1})	Dominant algae	Other common forms
	Sept. '78	(14)		10.0	Microcystis aeruginosa,	Some diatoms
	May '79	(14)	910		Tribonema sp.	Synedra sp., Anabaenopsis sp., Chroococcus sp.
Pawlo	1963–66	(3)	1000	10.0	Microcystis aeruginosa	
	1980	(3)				
Ashanghi	1937	(8)	1530	-	Chroococcus dispersus, Anabaenopsis circularis, Phormidium sp.	Pediastrum boryanum, Scenedesmus quadricauda, Staurastrum sp., Euastrum sp., Surirella linearis, Anomoeoneis sphaerophora, Peridinium sp.
Langano	1937	(7)			Anabaenopsis circularis, Pediastrum integrum, Oocystis sp., Scenedesmus quadricauda	Surirella ovalis, S. muelleri, Anomoeoneis sphaerophora, Glenodinium sp.
	Jan./Mar. '64	(3)	1810	14.5	Cryptomonas sp.	Aphanocapsa sp., Microcystis sp., Anabaenopsis sp., Glenodinium sp.
Bishoftu	1963–66	(3)	1830	20.0	Microcystis aeruginosa	
Biete	1937	(7)	2444	-	Peridineae	
Mengest	1964	(3)	2340	26.8	Microcystis aeruginosa	
	Apr. '80	(3)				
Turkana	1972–75	(15)	3071	24.2	Microcystis aeruginosa	Planctonema lauterborni, Botryococcus braunii, Surirella spp., Coscinodiscus (Thalassiosira) rudolfi
Kilotes	1963–66	(3)	5930	66.6	Chroococcus ? minutus;	v. small Spirulina sp.
	Mar. '80	(3)			(July 1964 only, Euglena sp.)	
Aranguadi	1963–66	(3)	6000	51.4	Spirulina platensis	?Glenodinium sp., Chroococcus ?minutus
Abiata	May '61	(3)	30000 (9)	210 (9)	Spirulina platensis, Oocystis sp.	?Anabaenopsis ?arnoldii
	Mar. '64	(3)	15800	166.4	Oocystis sp.	Spirulina platensis, Anabaenopsis ?arnoldii
Shala	1938	(7)	16671 (8)	-	Anomoeoneis sphaerophora	
	May '61	(3)	29500	200	v. sparse benthic diatoms	
	Mar. '64	(3)	19200	211		
Chitu	Aug. '66	(3)	28600	400	Spirulina platensis	
Metahara	May '61	(3)	72500	580	Spirulina platensis	Oscillatoria sp., Anabaenopsis ?arnoldii

(1) Brunelli & Cannicci (1940)
(2) Bini (1940)
(3) Original
(4) Talling & Rzoska (1967)
(5) Talling (1976)
(6) Gasse (1975)
(7) Cannicci & Almagià (1947)
(8) Loffredo & Maldura (1941)
(9) Talling & Talling (1965)
(10) Zanon (1941)
(11) Baxter & Golobitish (1970)
(12) Baxter *et al.* (1965)
(13) Brunelli & Cannicci (1941)
(14) Belay & Wood (1982)
(15) Hopson (ed.) (1982)

*Note. The algae named include many benthic forms. The Italian work often refers only to large groups (e.g. Cianoficeae) as dominant and taxonomic authorities are frequently not given in the literature quoted. Column 3 gives the reference for algal data, columns 4 and 5 include references for conductivity and alkalinity if different from column 3.

Table 7 gives the fewer determinations of biomass as chlorophyll *a*, often as single values or occasionally as ranges. These estimations are sufficient to show that considerable concentrations (>40 μg l^{-1}) can occur throughout the salinity series. Although the highest concentrations, >400 μg l^{-1}, were only recorded from lakes of high salinity (>5 g l^{-1}) and alkalinity (>50 meq l^{-1}), the deep yet saline L. Shala yielded low values. In gross chemical composition this lake is similar to the adjacent, shallow, and productive L. Abiata.

Talling & Talling (1965) drew attention to the importance of *Melosira* spp. in the plankton of their lower salinity (Class I) African lakes (conductivity $k_{20} < 600$ μS cm^{-1}) but rarely in more saline waters unless – as in L. Mohasi – the alkalinity is disproportionately low. Consistent with that is our failure to find *Melosira* spp. in any lake of higher alkalinity than L. Galilea (3.22 meq l^{-1}, conductivity 274 μS cm^{-1}), although there are early records (Zanon, 1942) from L. Awassa (~ 10 meq l^{-1}) and L. Abaya (~ 8 meq l^{-1}). However in Cl-dominated

Table 7. Algal biomass in some Ethiopian lakes.

Lake	Date	Reference	Chlorophyll *a* (μg l^{-1}) or general description
Tana	Mar. '64	(1) (2)	3.7
Zwei	1938	(3)	'clear water'
	Oct. '66	(4)	7
	Apr. '80	(5)	91
Hayq	1938	(3)	'limpida e verdastra'
	Jan. '69	(6)	1 'unusual clarity'
Awassa	1938	(3)	'scarce'
	Feb./Mar. '64	(7) (8)	'abundant'
	Apr. '80	(5)	40
Abaya	July '66	(9)	69
Chamo	July '66	(9)	89
	Sept. '78	(9)	'bloom'
	May '79	(9)	73
Pawlo	1964–66	(7)	1– 54
Ashanghi	1937	(10)	sparse
Langano	Oct. '66	(4)	7
	Mar. '80	(5)	7
	1980–81	(11)	1– 15
Bishoftu	1964–66	(7)	4– 34
Biete Mengest	Oct. '64	(7)	21
	Apr. '80	(7)	29
Kilotes	1964–66	(7) (12)	100– 412
	Mar. '80	(7)	535
Aranguadi	1964–66	(7) (12) (13)	400–5000
Abiata	Oct. '66	(4)	57
	Apr. '80	(5)	65
	1980–81	(11)	30– 75
Shala	Oct. '66	(4)	5
	Apr. '80	(5)	6
Chitu	Aug. '66	(7)	2600

(1) Talling (1976)
(2) Gasse *et al.* (1983)
(3) Cannicci & Almagià (1947)
(4) Wood *et al.* (1978)
(5) Belay & Wood (1984)
(6) Baxter & Golobitsh (1970)
(7) Original
(8) Baxter *et al.* (1965)
(9) Belay & Wood (1982)
(10) Loffredo & Maldura (1941)
(11) Wodajo & Belay (1984)
(12) Talling *et al.* (1973)
(13) Wood *et al.* (1984)

waters halophilic species of *Melosira* are known, such as *M. moniliformis* (Müll.) recorded from sediments of L. Afrera by Gasse (1974a). Similarly desmids have been found in Africa (as elsewhere) predominantly in waters of low alkalinity (<2.6 meq l^{-1}) and overall low salinity. In Ethiopian waters desmids (*Staurastrum* spp., *Eurastrum* spp.) have been reported only as far up the salinity series as L. Ashanghi ($k_{20} = 1500$ μS cm^{-1}, salinity 1.2 g l^{-1}).

The phytoflagellates appear to be most strongly represented in waters of low conductivity, which still contain significant concentrations of the bivalent cations, calcium and magnesium. Deficiency of these ions is known (e.g. Halldal, 1957; Nultsch, 1979) to inhibit flagellar activity. The (single) record of abundant flagellates in L. Galilea is particularly noteworthy in relation to the high concentrations of Ca^{2+} and Mg^{2+} plus high ratio of bivalent to monovalent cations, as is the isolated record of a *Mallomonas* sp. in L. Tana. However, both L. Langano (salinity <2 g l^{-1} and bivalent: monovalent cation ratio of only 0.02) and L. Aranguadi (a saline lake in Williams' definition, salinity ~ 5 g l^{-1}) have been found to contain species of *Glenodinium*, and a *Cryptomonas* sp. was common in L. Langano.

Of specialised alkaline-saline phytoplankton the alga *Spirulina platensis* (Fig. 13b) is perhaps the best known, strongly dominating the flora of L. Aranguadi (alkalinity ~ 50 meq l^{-1}), L. Chitu (alkalinity ~ 400 meq l^{-1}) and L. Metahara (alkalinity ~ 500 meq l^{-1}). Similar halo- or alkaphilic behaviour is known for it and probably conspecific organisms in soda lakes elsewhere. Examples in Africa include the Kanem soda lakes, salinity range 8.5–270 g l^{-1}: Iltis (1968); lakes Nakuru, Elmenteita, Reshitani, and Big Momela with alkalinity 122, 107, 164 and 168 meq l^{-1} respectively: Melack & Kilham (1974); L. Simbi, alkalinity 260 meq l^{-1}: Melack (1979); L. Yoan, alkalinity 480 meq l^{-1}: Léonard & Compère (1967); and others exist in S. America (e.g. L. Huacachina, alkalinity 106 meq l^{-1}: Löffler, 1960; Thomasson, 1960). In dominating those lakes it also achieves very dense populations which, for L. Aranguadi, have been considered in Wood (1968: seasonal data reproduced in Talling, 1985) and Talling *et al.* (1973). Occurrence is also known (Al-Saadi, Ergaschev & Pankow, 1981) in saline waters of low alkalinity such as the Shatt al-Arab, Iraq (alkalinity <5 meq l^{-1}: Talling, 1980). A physiological basis for its salinity tolerance, in the cellular accumulation of glucosyl glycerol as osmoticum, has been recently established (Warr *et al.*, 1985). The Ethiopian lakes Kilotes and Aranguadi are also similar to lakes Nakuru and Elmenteita (Kenya) in having a very small-celled coccoid blue-green alga resembling *Chroococcus minutus* in their phytoplankton. In L. Kilotes it was the almost continuous dominant during 3 years of study, reaching population densities over 500 μg chlorophyll *a* l^{-1}. In L. Aranguadi it was a minor but consistent component of the flora strongly dominated by *Spirulina platensis*.

A third cyanophyte commonly associated with very saline, alkaline water is *Anabaenopsis arnoldii* Aptekarj (see e.g. Melack & Kilham, 1974), which we have found in L. Abiata (which also contained in 1961 a significant amount of *Spirulina platensis*, see Fig. 13b) and L. Metahara. Unexpectedly we found an *Oocystis* sp. (Fig. 13b) to be the dominant phytoplankter in L. Abiata in 1961 and 1964, a genus not seen elsewhere in Ethiopia in more saline waters than L. Langano and L. Ashanghi by either the Italian workers or ourselves, although two *Oocystis* spp. are reported as abundant or common in three saline Canadian lakes (Hammer *et al.*, 1983). A hot-spring tributary of L. Shala was found, in 1961, to contain quantities of the known halophilic but non-planktonic cyanophytes *Spirulina subsalsa* Oerst and *Synechococcus elongatus* Näg. f. *thermalis* (Geitler) (Fig. 13c). Another algal group, the diatoms, provides many examples of non-planktonic alka-halophilic species such as *Anomoeoneis sphaerophora* (Kütz.) Pfitzer (Gasse *et al.*, 1983), and the planktonic *Thalassiosira rudolfi* (*Coscinodiscus rudolfi* Bachm.) known from L. Turkana and L. Shala (Gasse *et al.*, 1983).

Some phytoplankters appear to be distributed only in waters of intermediate salinity and alkalinity. One is the filamentous green alga *Planctonema lauterborni* Schmidle, abundant in L. Turkana and, elsewhere in East Africa, seen only in L. Tanganyika (Hecky *et al.*, 1978), L. Edward and L. Kitangiri (Hecky & Kling in press; Talling unpublished). These lakes fall in the conductivity range 600 to 3000 μS

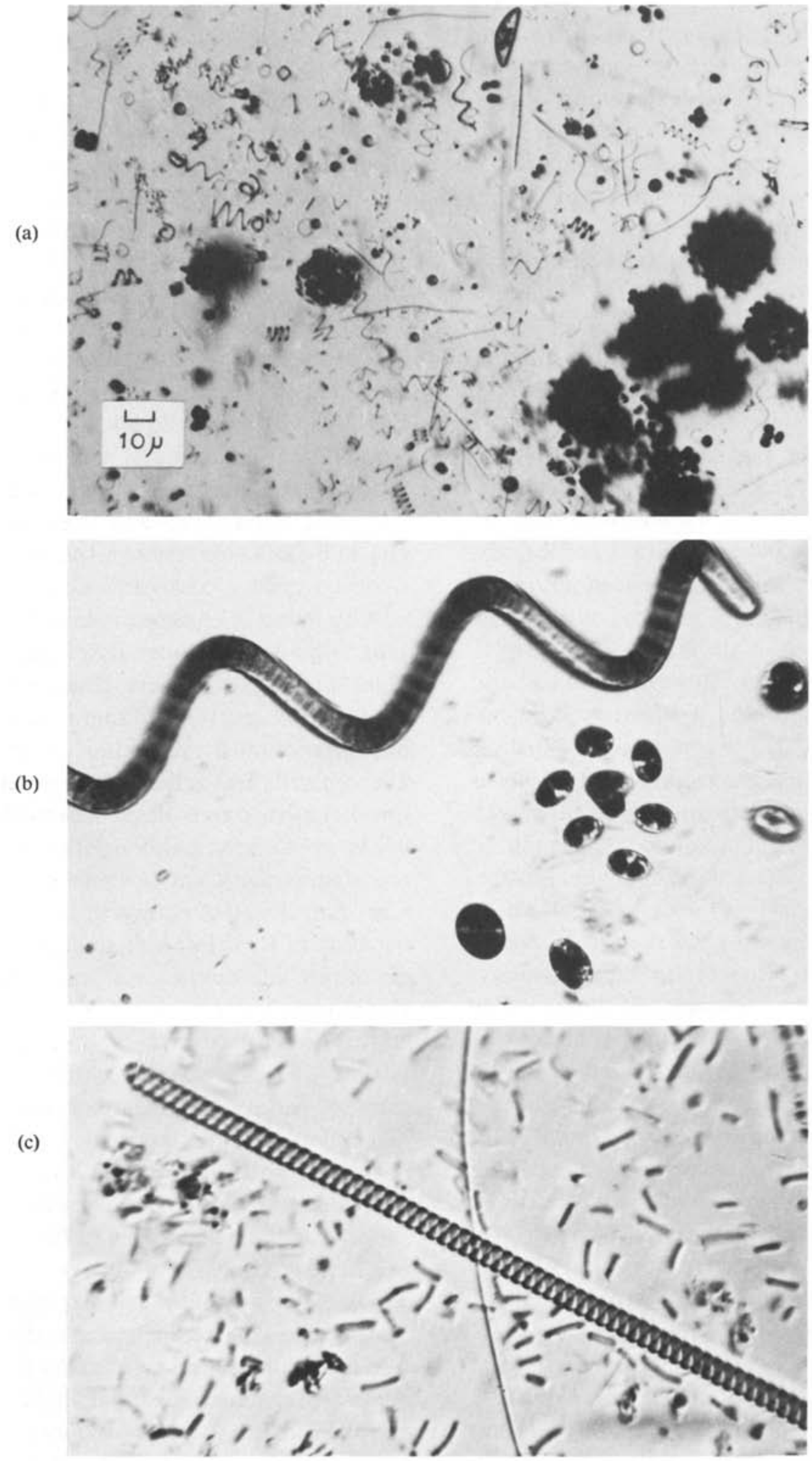

Fig. 13. Photomicrographs of iodine-sedimented phytoplankton from (a) L. Awassa, of low salinity, dominants *Spirulina* and *Microcystis* spp., (b) L. Abiata, of high salinity, dominants *Spirulina platensis* and *Oocystis* sp., and (c) L. Shala saline hot spring showing *Spirulina subsalsa* and *Synechococcus elongatus* f. *thermalis*.

cm^{-1}. For diatoms, Gasse *et al.* (1983) have distinguished assemblages of species characteristic of intermediate as well as low and high levels of salinity and alkalinity. In Ethiopia there is scant recorded modern development of phytoplankton with strong representation of the diatom genus *Nitzschia*, which in East and Central Africa is known to often succeed a *Melosira*-plankton in transition to lakes of higher alkalinity > c. 6 meq l^{-1} (Hustedt, 1949; Talling & Talling, 1965; Richardson, 1968; Gasse *et al.*, 1983). However it is well represented in the plankton of L. Abaya (Brunelli & Cannicci, 1941; Zanon, 1942; Gasse *et al.*, 1983) and by microfossils in some Ethiopian lake sediments (e.g. lakes Abhe and Afrera: Gasse, 1977a, b; Gasse & Street, 1978b).

An important cyanophyte which has generally a broad tolerance of salinity but whose upper limit of salinity in the present series appears to be about 3 g l^{-1}, is *Microcystis aeruginosa*. This, as *M. aeruginosa* f. *flos-aquae* or *M. aeruginosa* f. *aeruginosa*, sensu Komárek (1958), is present, often as a strong and long-term dominant, in lakes in the series from L. Zwei (salinity ~0.3 g l^{-1}) to L. Turkana (~3 g l^{-1}). Certainly in the three less saline of the Bishoftu crater lakes (L. Pawlo, L. Bishoftu and L. Biete Mengest) *M. aeruginosa* was the dominant phytoplankter during the period 1963–66. Hammer *et al.* (1983) noted a much wider salinity tolerance of *Microcystis aeruginosa* in the ionically dissimilar Saskatchewan lakes, where they reported it in relatively low-alkalinity waters with dominant ions Na^+, Mg^{2+} and SO_4^{2-} (Hammer, 1978) up to 100 g l^{-1}.

Within Ethiopia there is a lesser represention of another ionic type with Cl^- rather than HCO_3^- + CO_3^{2+} as dominant anion. Floristic information is available only for largely non-planktonic diatoms (Gasse *et al.*, 1983; Gasse, 1986a, b), for which Gasse *et al.* distinguish a Group V by correspondence analysis that derives mainly from the Afar region. Most of the characteristic species usually inhabit littoral marine environments, but the sub-group VB derives from relatively low salinity waters of the Wadi Kelou (Afar) of conductivity <3000 μS cm^{-1}.

Discussion

The series of increasingly saline Ethiopian waters reported here illustrated a continuum, with the delineation of a saline class somewhat arbitrary. It does however fit into well-established pattern of African inland waters characterised principally by increasing concentrations of sodium and bicarbonate-carbonate, as described by Talling & Talling (1965), extended by Eugster (1970), Hecky & Kilham (1973), Kilham & Hecky (1973), and Cerling (1979). Talling & Talling drew attention to the desirability of further comparative survey of waters within the alkalinity range 25–100 meq l^{-1}, 'chiefly found in small and little known crater lakes'. Such information is now available from the present Ethiopian series, as well as crater lakes elsewhere in East Africa (e.g. the Basotu crater lakes: Kilham, 1984; L. Simbi: Melack, 1979; Finlay *et al.*, 1986).

Evidence has been given that the Ethiopian salinity series is largely determined by water input-output relations and hence evaporative concentration rather than by large local injections of geochemically juvenile material. This is also the interpretation of Cerling (1979) for lakes of the Eastern Rift generally, although volcanic carbonatites are widespread (Holmes, 1965), such as the sodium carbonate lava and ash from the volcano Oldoinyo Lengai (Dawson, 1962, 1964). It differs from the situation in the Western Rift with other inputs (e.g. K^+, Mg^{2+}) as from the Virunga volcanic field (Talling & Talling, 1965; Arad & Morton, 1969). Nevertheless the concentration process may involve saline springs, thermal reflux pathways, and the alternate deposition and leaching of non-marine evaporites. Past conditions of overflow from basins now closed are clearly relevant, both for lowering salinity in upstream lakes (e.g. L. Chamo) and for promoting evaporites and lake salinity downstream (e.g. Chew Bahir [Stephanie]). In the latter respect the past overflow (Grove *et al.*, 1975) from a major rift basin (Fig. 2) encompassing the present lakes Zwei, Langano, Abiata and Shala, to the Awash River and the terminal L. Abhe, is noteworthy. Subsequent falls of lake level (evaporative contraction) since about 5000 BP have been very large in several closed lake basins, as of lakes Shala (c. 110 m), Abhe (c. 150 m), Assal (c.

300 m), and Turkana (c. 60 m).

Given that saline soda lakes usually support very dense and very active populations of phytoplankton, it might be asked whether the more saline sodium carbonate-dominated lake waters of evaporative origin are intrinsically productive. There are at least two positive considerations. A common correlate of productive status is phosphorus concentration and, though loss processes exist, in Na^+-rich and Ca^{2+}-poor waters phosphate may be passively concentrated by evaporation to high concentrations. Thus measured values of *total* P concentration in four Ethiopian soda lakes at or above the salinity level of L. Turkana (0.89–1.1 mg l^{-1}: from Talling & Talling, 1965) correspond to a ratio to alkalinity of 4–106 μg P per meq, no larger than is commonly found in dilute waters of 'low' P content. Also, especially in volcanic areas, the soils and hence inflows may be phosphate-rich. However, in the productive Kenyan soda lakes of Elmenteita and Nakuru there are records of low concentrations of soluble reactive phosphate (Peters & MacIntyre, 1976; Vareschi, 1982), and in that of Sonachi there is experimental evidence from P additions that phosphate can limit concentrations of phytoplankton biomass (Melack *et al.*, 1982; cf. also Kalff, 1983).

In Ethiopia, L. Kilotes, L. Aranguadi, L. Shala and L. Chitu all contain very high concentrations of soluble reactive phosphate. Both the standing crops of phytoplankton and the rates of photosynthesis for L. Kilotes and L. Aranguadi have been shown to be high (L. Kilotes biomass in surface water 100–535 μg chl *a* l^{-1}, gross areal photosynthesis 0.5–2.4 g 0_2 m^{-2} h^{-1}; Talling *et al.*, 1973). L. Abiata, with lower soluble reactive phosphate, is less but still very productive (30–75 μg chl *a* l^{-1} and 0.5 g O_2 m^{-2} h^{-1}: Belay & Wood, 1984), while the concentration of biomass in L. Chitu (2600 μg chl *a* l^{-1}) was closely comparable with that of L. Aranguadi. Melack & Kilham (1974), Melack (1979, 1981), and Vareschi (1982) have reported similar elevated values of biomass concentration and areal photosynthesis for some Kenyan soda lakes which typically show high concentrations of soluble reactive phosphate. More generally for productive shallow lakes, but excluding L. Kilotes, there is evidence (reported by Golterman & Kouwe, 1980) for an empirical relationship between total phosphorus concentration (P_{tot}, in μg l^{-1}) and the maximum light-saturated rate of photosynthesis per unit water volume ([A_{max}]max, in mg O_2 l^{-1} h^{-1}), namely [A_{max}max = 11 × P_{tot}.

Talling *et al.* (1973) reasoned that among the other chemical features of soda lakes which favour dense but active populations are the large reserves of carbon dioxide even at pH values above 10. The significance of this feature *in situ* (*extra vitro*) depends on the rate of CO_2-transfer by vertical mixing between the illuminated CO_2-consuming and dark CO_2-producing layers. Restrictive density gradients are often diurnally pronounced, especially in very productive and sheltered crater lakes like L. Aranguadi (Talling *et al.*, 1973; Wood *et al.*, 1976) and the Kenyan lakes Simbi (Melack, 1979; Finlay *et al.*, 1986, and personal observations) and Sonachi (Melack, 1981). They will be enhanced by the localized power consumption in very dense and absorptive algal populations, as noted by Nakamoto (1975) for dense populations of a dinoflagellate elsewhere.

Either dense phytoplankton or large background light attenuance (also common in soda lakes) can induce another major constraint, postulated by Moss & Moss (1969) for L. Chilwa in Malawi and by Kalff (1983) for Kenyan soda lakes, where dense surface crops, extreme self-shading and euphotic depths as little as 0.15 m probably set a limit to biomass growth. In the large exposed and exceptionally deep saline lake of L. Shala, where ill-defined thermal discontinuities have been found both by Baumann *et al.* (1975) and ourselves (Baxter *et al.*, 1965) as deep as 50–70 m and beyond, and where light attenuation even in the presence of low crops is still very high (euphotic depth 5 m, with 6 μg l^{-1} chlorophyll *a*: Belay & Wood, 1984), it seems likely that the lake must be considered optically deep (Wood *et al.*, 1978) and light a major constraint. If so, the low productivity of this, an exceptionally deep soda lake (Melack, 1983), is compatible with a potential chemical fertility; clearly experimental testing, as with shallow ponds of L. Shala water, is required.

Very low phytoplankton densities are also reported qualitatively from another terminal, very saline, but moderately shallow soda lake, L. Abhe (Gasse & Street, 1978b), and are evidence against an intrinsic chemical fertility of soda lakes. However there appears to be no information on the phosphorus content of this lake; the salinity, although high, is only about 1.4 times higher than reported for the productive L. Nakuru (Kenya) in 1961 by Talling & Talling (1965). Also described as unproductive are the waters of the very saline and Cl^- dominated lakes Afrera and Assal.

In traversing the salinity series, both salinity and its major ionic correlates (e.g. elevated pH, loss of divalent cations) can co-influence the floristic composition of phytoplankton. Response to higher salinity is likely to be governed by compensatory cellular osmotica, as known elsewhere (Warr *et al.*, 1985) for *Spirulina platensis*. Response to divalent cations may be partly specific to flagellated forms, for which there are supporting indications from the abundance of chrysomonads and dinoflagellates in relatively Ca^{2+} and Mg^{2+}-rich lakes of the western rift such as Albert (Talling, 1963), Edward (Hecky & Kling, 1986), Kivu (Hecky & Kling, 1986), and Tanganyika (Hecky & Kling, 1981, 1986). In the lakes of Ethiopia and East Africa generally (including L. Victoria: Talling, 1966, 1986), a paucity of flagellates is often associated with a rich development of small blue-green algae (cf. Fig. 13a) whose possible chemical control may then be relevant to flagellate distributions. For further progress experimental studies will clearly be important. However, Gasse has also shown the gains possible by more objective community analysis, and the value – also valid for geochemistry (Cerling, 1979) – in associating the Ethiopian information with that from East Africa generally (Gasse & Tekaia, 1983; Gasse *et al.*, 1983; Gasse, 1986a). The last point is also illustrated by Fryer & Talling (1986) in relation to chemical control of the occurrence of *Melosira* spp. and *Spirulina platensis*.

Historically, most discussion of salinity tolerance in algal ecology has related to a 'Halobiensystem' in Cl^--dominated waters (e.g. Kolbe, 1932; Hustedt, 1953; and Patrick, 1977 for diatoms), from which the majority of Ethiopian and East African waters differ. In most of these waters pH, alkalinity, and salinity are strongly correlated, so that a succesful relation of species distribution to pH (cf. Gasse & Tekaia, 1983; Gasse *et al.*, 1983) does not preclude a causal relationship to another factor or factor-combination. Thus the relative significance of higher salinity, higher alkalinity, higher pH, reduced free CO_2 or another correlate in restricting the occurrence of most desmids and *Melosira* spp. requires further systematic study both by experiment (e.g. Moss, 1973) and environmental comparison (e.g. Talling & Talling, 1965; Kilham & Kilham, 1975; Gasse, 1986a). At present these types of evidence suggest that salinity itself is not the most important factor, an interpretation supported by the contrast between the present algal-salinity distributions and the much wider ones in the low alkalinity saline lakes of Saskatchewan (Hammer, 1978; Hammer *et al.*, 1983).

In a region where chemical diversity is predominantly related to past evaporative concentration, bio-distributional evidence from many sites can be more readily employed for the reconstruction of lake history from micro-fossil evidence at one site. This approach has been employed with diatom analysis for lakes Abhe and Afrera (Gasse, 1974a, b, 1975, 1977a, b, 1980, 1986a; Gasse & Delibrias, 1976; Gasse & Street, 1978b), L. Abiata (Gasse & Descourtieux, 1979), and for L. Turkana (Richardson in Cerling, 1979); thus the abundance of various *Melosira* spp. has indicated earlier phases of lower salinity from which the more saline present conditions and floras have evolved.

The significance of other organisms present in Ethiopian lakes or lake sediments as indicators of salinity or its correlates is largely beyond our present scope. As examples, the copepod *Paradiaptomus africanus* (Daday) (*Lovenula africana* Daday) is abundant in some soda lakes (e.g. Aranguadi, Kilotes) in Ethiopia as in East Africa (LaBarbera & Kilham, 1974); molluscs are largely lacking from lakes of higher alkalinity than L. Turkana (Brown, 1980); insects of soda lakes include a strong development of corixids in L. Abiata, and of one chironomid in L. Shala (Thienemann, in Cannicci & Almagià, 1947); excepting L. Abiata, fish appear to be generally absent from soda lakes of alkalinity > 100 meq l^{-1}, with the exception of the specialist cichlid *Danakilia franchetti* (Vinciguerra) of L. Afrera, a parallel to *Oreochromis alcalicus* (Hilgendorf) known from East Africa. The significance of some of these groups for the reconstruction of lake history during evaporative concentration is discussed by Grove *et al.* (1979) and Cerling (1979) with reference to lakes Shala and Turkana.

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