

The ecology of Lake Nakuru (Kenya)

IV. Biomass and distribution of consumer organisms

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Summary. Consumer biomass and spatial distribution in the equatorial alkaline-saline Lake Nakuru were studied from 1972–1976. These data will provide the basis for estimating feeding and production rates and for quantifying energy flow at the consumer level. Two of the main consumers, the Lesser Flamingo (*Phoeniconaias minor*) and the Soda Tilapia (*Sarotherodon alcalicus grahami*), were covered by earlier papers. The biomass of the only planktonic crustacean, the copepod *Lovenula* (= *Paradiaptomus*) *africana* was very high (1.5 gDW (dry weight) · m⁻³, mean in 1972/73) in comparison with other tropical lakes. *Lovenula* was absent in 1974 and 1975, and at very low levels (0.1–0.4 gDW · m⁻³) in part of 1976. Among the rotifers *Brachionus dimidiatus* dominated in 1972/73 (~0.2 gDW · m⁻³), but was outnumbered by *B. plicatilis* throughout most of 1974 to 1976 (mean total rotifer biomass 1.4 gDW · m⁻³, peak densities 7 gDW · m⁻³); during high salinity periods (>20‰) *Hexarthra jenkiniae* occurred in very low numbers. For short periods rotifers can be the dominant species of L. Nakuru. Aquatic heteroptera (four species) played a minor role: they contributed 0.4% to total consumer biomass in 1972/73; in 1974–1976 the lake had no aquatic heteroptera. Benthic biomass (0.4 gDW · m⁻²) was within the range of other tropical lakes, it consisted almost exclusively of *Leptochironomus deribae*. Bird counts of the twelve most important species are given for the years 1972–1974: *Pelecanus onocrotalus* accounts for ~90% of the biomass (0.44 gDW · m⁻³, mean 1972/73) with peak densities of almost 20,000 birds. – The consumer organisms covered by this and the two preceding papers represent >99% of L. Nakuru's consumer biomass. Population dynamics of various consumer species are discussed.

Introduction

Lake Nakuru is a shallow alkaline-saline lake in the eastern rift valley of Kenya. An outstanding characteristic of the lake is its biological simplicity: only four species account for >99% of the lake's total biomass, making the lake a suitable object for ecosystem research.

The aim of this paper is to describe the changes in biomass and distribution of the major consumer species to provide the basic data needed for estimating feeding and production rates and for quantifying energy flow at the

consumer level. Papers I–III dealt with abiotic factors, energy input and primary production (Vareschi 1982), with biomass, distribution and feeding of the Lesser Flamingo *Phoeniconaias minor* and with the distribution and abundance of the Soda Tilapia *Sarotherodon* (= *Tilapia*) *alcalicus grahami* (Vareschi 1978, 1979). This paper surveys copepods (*Lovenula africana*), rotifers (*Brachionus dimidiatus* and *B. plicatilis*), aquatic heteroptera (*Micronecta jenkiniae*, *M. scutellaris* and *Anisops varia*), benthos (*Leptochironomus deribae* and *Tanytarsus horni*) and birds (mainly *Pelecanus onocrotalus*). The consumer organisms covered by this and the preceding papers represent >99% of the lake's consumer biomass (excluding decomposers).

Two further publications (Vareschi and Jacobs 1983 and in prep.) will deal with feeding and production of these species and present a synopsis of our present knowledge of the ecosystem.

1. Copepods

Only one *Crustacea* species inhabits L. Nakuru: a planktonic diaptomid which Kiefer (pers. comm) indentified to be *Lovenula africana* Daday (= *Paradiaptomus biramata* Lowndes = *Paradiaptomus africanus* Daday). Lowndes (1933) found this copepod only in L. Elmenteita but LaBarbera and Kilham (1974) established a wide distribution in 11 different alkaline-saline lakes of East and Central Africa.

Methods

In order to estimate temporal biomass changes of all lake organisms, samples were taken at 19 stations in monthly intervals. 14 shore sampling stations were placed at two kilometer intervals about 200 m off shore (due to lake level changes the exact site varied, though always the same shore region was sampled). 5 midlake sample stations were placed at equal distances from shore and from one another (Fig. 1; in midlake less samples were necessary because of a more homogenous distribution of all organisms). Copepods were collected using a plankton net (Ø 25 cm) hauled vertically from just above the sediments to the surface at the 19 sampling stations (Fig. 1). A net with mesh size 300 µ was used for quantitative sampling of adults and the larger copepodit stages, but nauplia and eggs passed this net. From parallel hauls with a 56 µ net relative proportions of adults: copepodits: nauplia: eggs were established for each biomass estimate.

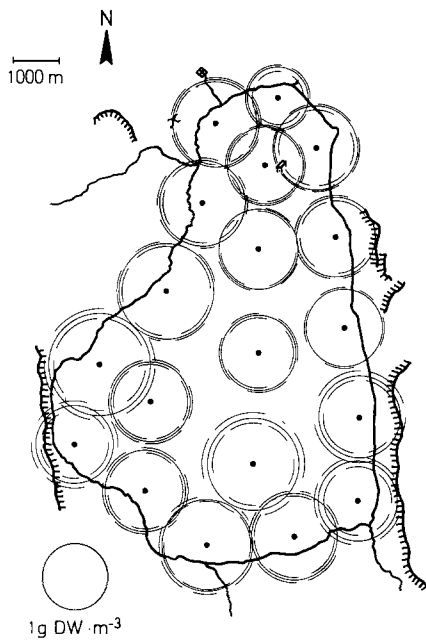


Fig. 1. Mean horizontal distribution of copepods (*Lovenula* [= *Paradiaptomus*] *africana*) in L. Nakuru in April 1972 to December 1973. The areas encircled by solid lines represent biomass ($\text{gDW} \cdot \text{m}^{-3}$), broken lines indicate SEs at the 19 sampling points. On the bottom left an area indicating $1 \text{ gDW} \cdot \text{m}^{-3}$ is given for reference

To reduce time spent on counting each sample, the following method was adopted: The volume of the copepods of each sample was measured using volumetric cylinders (\varnothing 15 mm). The numbers of adults and copepodites per sample were calculated from sample volume, relative proportions of adults and copepodites, and from an estimate of the mean volume one adult copepod (\bar{V}_A) and one copepodite (\bar{V}_C) occupied in the volumetric cylinder. These mean volumes were derived from numbers of adults and copepodites and the volumes of 19 samples counted completely. As \bar{V}_A and \bar{V}_C changed during 1972–1973, mean carapax length of a random sample of at least 50 adults (\bar{L}_A) and 50 copepodites (\bar{L}_C) was measured for each biomass estimate. Mean \bar{L}_A^{-3} and \bar{L}_C^{-3} was taken as approximately proportional to individual volume and \bar{V}_A and \bar{V}_C could be corrected accordingly by comparison with the original values of \bar{L}_A^{-3} and \bar{L}_C^{-3} in the 19 samples counted completely. Nauplia and the first 2 copepodite stages contributed insignificantly to total sample volume (<3%) and were therefore not taken into account. The calorific values ($\text{cal} \cdot \text{gDW}^{-1}$) given in the literature for copepods range from 4,850–5,270 (*Cyclopoida*, Vijverberg and Frank 1976), 5,294 (*Diaptomidae*, Cummins and Wuycheck 1971) and 5,022–6,307 (*Diaptomus*, Schindler et al. 1971). Since no data on the energy content of *Lovenula* are available, the calorific value was assumed to be 5,200 cal per g dry weight.

Samples for establishing vertical distribution patterns and vertical migration were collected from 0, 25, 50, 100, 180 and 230 cm depth using a handpump ($30 \text{ l} \cdot \text{min}^{-1}$) with a rubber hose leading to a 15 cm funnel. 10 l was pumped from each depth and screened by 56μ netting. Samples were preserved and counted completely.

Error estimates. Ten samples were taken three times within minutes at the same location to test for reproducibility.

The resulting standard error (SE) was 4% of the mean. Volume measurements of the same sample had a SE of <1% of the mean and 10 countings of the adult/copepod relation had a SE of 2.1%. The mean SE of the hauls at the 19 sampling stations was 17%. SE of dry weight estimates was assumed to be 5%. The resulting total SE of copepod biomass estimates was 18.3% (calculated as the square root of the summed squares of SEs).

Results and discussion

Vertical distribution. The vertical distribution pattern of *L. africana* was established in 4 h intervals during a 24 h period in April, May and June 1972. Though steep gradients of light, temperature and oxygen concentration are common, no distinct diurnal migration pattern could be detected in the 2.3 m water column, apart from a higher concentration of nauplia and copepodites near the surface in the evening and at night and an avoidance of depths >200 cm after midnight: water close to sediments usually becomes anoxic ($<1 \sim 0 \text{ mgO}_2 \cdot \text{l}^{-1}$) for about 6 h every night (Vareschi 1982). Chaston (1969) showed that nauplia can tolerate anaerobic conditions for only 1 h while older stages are less sensitive and adults may even survive for many hours without oxygen.

Horizontal distribution. Copepod samples taken at the 19 regular sampling points showed high variations (mean coefficient of variation [CV]=74%). But if the means of samples at each of the 19 sampling points are considered, copepod biomass appears homogeneously distributed (Fig. 1), indicating no permanent preference for any lake regions.

Temporal changes. Though copepod biomass ($\text{gDW} \cdot \text{m}^{-3}$) varied considerably in 1972 (from 1.2–2.6, mean $1.8 \pm 0.5 \text{ SE}$, $N=8$; see Table 1), a decreasing tendency is obvious (Fig. 2). In 1973 copepod biomass was considerably lower than in 1972 but it stayed relatively stable (mean $1.1 \pm 0.2 \text{ SE}$, $N=7$), followed by a complete breakdown of the population in January/February 1974 (27.12.1973: 1.2; 1.2.74: 0.8; 6.2.74: 0.001; March 74: nil). Copepods were virtually absent throughout 1974 and 1975: only in November of both years a few isolated examples were found by net dragging (biomass $\leq 0.0001 \text{ mgDW} \cdot \text{m}^{-3}$). A partial recovery of the population was indicated in March–May 1976 but in August 1978 the lake was once again without copepods. The mean female/male relation was 54%/46%, and $75 \pm 3\%$ (SE; $N=14$) of the females carried eggs. Egg production was declining by the end of 1973 (September 65%, November 63%, December 46%).

Although comparable data on zooplankton biomass of tropical lakes are scarce, it is apparent that L. Nakuru has a relatively high standing crop of copepods: for L. George (Uganda), Burgis (1974) reported a mean crustacean biomass ($\text{gDW} \cdot \text{m}^{-3}$) of 0.37 (dominated by *Thermocyclops hyalinus*), for the three different ecological regions of L. Chad (Chad) Carmouz et al. (1972) estimated 0.105, 0.24 and 0.35 (composed of 50% copepods, 30% Cladocera, 15% rotifers; Lévêque et al. 1972). In temperate regions only summer maxima are in the range of mean Nakuru values, e.g. 1.03 in Loch Leven (Burgis and Walker 1972) or 0.97 in Queen Mary Reserve (Steel et al. 1972; annual mean 0.025).

The monthly ups and downs of copepod biomass in

Table 1. Mean density and biomass of copepods (*Lovenula* (= *Paradiaptomus*) *africana*), with SE. Numbers after the years indicate months of sampling. From March 74 – August 1976 no copepods were in the lake with the exception of January–July 1976. In 1976 only the 300 μ net was used, therefore nauplii, smaller copepodites and part of the eggs were missed. Data for 1975/76 are from T. and V. Schwan (pers. comm.)

Year	Numbers \cdot m ⁻³				Biomass		
	Adults	Copepodites	Nauplii	Eggs	gDW \cdot m ⁻²	gDW \cdot m ⁻³	kJ \cdot m ⁻³
1972 (4–12)	10,530 \pm 930	1,930 \pm 210	36,440 \pm 4,400	143,760 \pm 14,100	4.58	1.81 \pm 0.15	39.4
1973 (1–12)	6,700 \pm 370	1,880 \pm 340	12,900 \pm 2,800	91,320 \pm 6,780	2.30	1.15 \pm 0.06	25.0
1976 (1–8)	930 \pm 60	390 \pm 30	–	4,200 \pm 260	0.11	0.16	3.4
1978 (8)	1,020	1,638	–	5,280	0.62	0.20	4.4

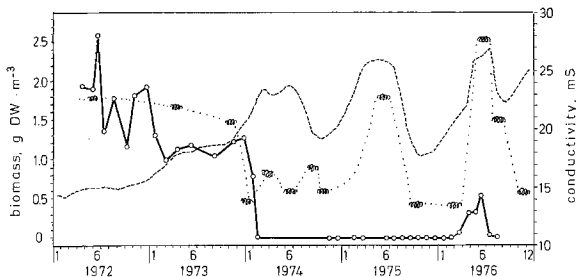


Fig. 2. Mean biomass of copepods (*Lovenula* (= *Paradiaptomus*) *africana*) in 1972–1976. The solid line gives biomass of copepods (left y-axis, gDW \cdot m⁻³), the dashed line conductivity (right y-axis, mS (= mhos \cdot cm⁻²), 20° C; conductivity was calculated from lake level data (Vareschi 1982). Algal biomass levels are indicated by *Spirulina* filaments (dotted line, left y-axis, gDW \cdot m⁻³ \cdot 10⁻²; high algal biomass in mid-1975 was mainly due to *Anabaenopsis* and single-celled cyanophytes rather than *Spirulina*). Data after November 1974 are from T. and V. Schwan (pers. comm.)

1972 (up to 50% change within 1 month) are difficult to account for, as the predators feeding on copepods did not show corresponding fluctuations and no other relevant parameters changed in parallel. It is also unlikely that the total SE of the biomass estimates (18.3%) could have caused such variations. Besides, in 1973 the fluctuations were much smaller. The breakdown of the copepod population in early 1974 could be interpreted as an effect of increasing salinities caused by evaporation (Fig. 2). LaBarbera and Kilham (1974) studied copepod distribution in relation to conductivity in 48 African lakes. Most copepods were restricted to definite salinity ranges with *Lovenula africana* occupying the highest range of 3,350–15,000 μ S. Only one lake with a conductivity of > 15,000 μ S was included in the study (L. Eyasi, 23,000 μ S, no copepods), so that the upper range cannot be regarded as a definite limit for *Lovenula africana*. This is confirmed by our data (Fig. 2): at 15,000 μ S the *Lovenula* population was at its best but coinciding with the conductivity increase in January/February 1974 (21,200 μ S \rightarrow 25,300 μ S) the copepod population collapsed. Kilham and Hecky (1973) and LaBarbera and Kilham (1974) suggested that the generally high fluoride concentration of closed basin rift lakes might also influence copepod distribution. They found *Lovenula africana* in lakes with up to 437 mg F \cdot l⁻¹, which is well above L. Nakuru concentrations during 1972–1978 (\sim 300 mg F \cdot l⁻¹ at 27,000 μ S).

In 1974/75 and in 1978 decreasing conductivities did

not bring a recovery of the copepod population and in 1976 copepods recurred, though conductivities were then rising from 19,400 μ S to 25,900 μ S (Fig. 2; but a further increase again coincided with a collapse of the copepod population). Therefore *L. africana* population dynamics must be influenced by additional parameters, in particular by biological interactions with other species: the main food organism is the cyanophyte *Spirulina platensis* ($\varnothing \sim$ 30 μ). From early December 1973 to February 1974 algal biomass dropped from 150 to 50 gDW \cdot m⁻³, and the contribution of *S. platensis* to total algal biomass from 73% to 5%. In parallel another considerably larger *Spirulina*-form ($\varnothing \sim$ 80 μ), probably too large to be filtered by *L. africana*, gained in relative importance. In mid 1975 algal biomass was high again but *Spirulina platensis* was almost absent and conductivities were probably near the toleration limit for *L. africana*. In April 1976 algal biomass recovered again (> 200 gDW \cdot m⁻³) with *S. platensis* and *Anabaenopsis* of similar size dominating; this was followed by an algal breakdown in July 1976. In parallel the *L. africana* population had a short recovery to almost 50% of the 1973 density, followed by a fall to zero density in July/August 1976 (Fig. 2; all data on algal density and species composition from Vareschi 1982 and unpubl.). From the data presented here conductivities of > 25,000 μ S may be limiting the development of *L. africana* populations, but the availability of the main food organism *S. platensis* seems at least of equal importance.

2. Rotifers

The characteristic rotifers of L. Nakuru are *Brachionus dimidiatus* Bryce and *B. plicatilis* Müller. *Hexarthra jenkiniae* de Beauchamp, *Cephalodella obvia* Donner and *C. catellina*

Table 2. Measurements of rotifers, with SE (N = 30–50). For mode of calculation see p. 73

	Length (μ m)	Width (μ m)	Volume (μ m ³ \cdot 10 ⁶)	Dry weight (μ g)
<i>B. dimidiatus</i>				
adult	109.6 \pm 2.5	74.1 \pm 0.7	0.24	0.022
egg	71.5 \pm 7.5	51.5 \pm 6.5	0.14	0.012
<i>B. plicatilis</i>				
adult	239 \pm 6	169 \pm 5	2.68	0.24
egg	170 \pm 4	122 \pm 33	1.00	0.09
<i>H. jenkiniae</i>	110 \pm 3.5	75 \pm 2	0.49	0.044

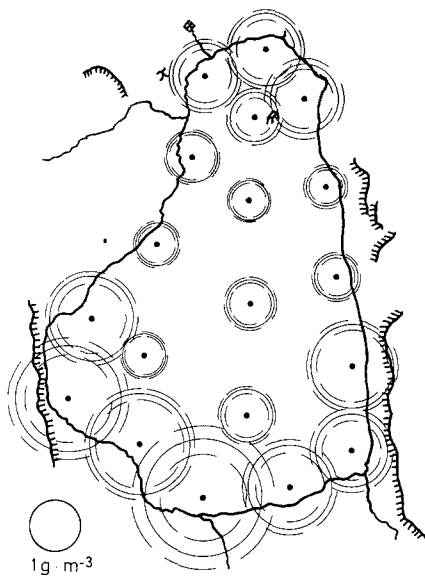


Fig. 3. Mean horizontal distribution of rotifers (*Brachionus dimidiatus*, *B. plicatilis*, *Hexarthra jenkiniae*), 1972/76; see Fig. 1 for explanation

major *Zawadowsky* occur relatively seldom. This rotifer spectrum seems to be characteristic for saline-alkaline lakes throughout the world: the same species were found in Australian salt lakes (Walker 1973) and in most natron temporary ponds and permanent lakes of Kanem, Chad (Pourriot et al. 1967). De Beauchamp (1932) originally described *Hexarthra* as *Pedalia jenkiniae*, and his *Cephalodella elmenteita* was later recognized to be *C. catellina major* (Koste pers. comm.). Koste (pers. comm.) and Ruttner-Kolisko (pers. comm.) identified *B. dimidiatus* from the Nakuru samples as *B. dimidiatus f. inermis* Schmarda. Our samples of *H. jenkiniae* and *C. obvia* differed from the types in several aspects and were classified by Koste as *H. jenkiniae f. nakuru* and *C. obvia nakuriensis* (Koste 1977 and pers. comm.).

Methods

Rotifer counts were based on monthly samples at the 19 sampling stations (p. 70 and Fig. 3). An open 1-l-bottle was raised at constant speed from bottom to surface. At the lab the exact volume of water drawn was measured, the

rotifers were retained by 31.5 μ netting (the smallest eggs of *B. dimidiatus* measured 40–60 μ), they were stained with methylen blue to facilitate counting, and rinsed into a Petri-dish with a 1 mm grid marked on the bottom. An area of 20–1,600 mm² or at least 100 rotifers per sample were counted. Loose eggs could be identified by size and were assigned accordingly. Lorica measurements were taken using a microscopic drawing tube. Occasional thorns were not included in length measurements.

Measurement of rotifer dry weight is quite intricate and could not be performed at our field lab. The dry weight of single *Brachionus* was therefore estimated from length and width of the lorica using the formula of a half cylinder ($V = w^2 \cdot l \cdot \pi \cdot 8^{-1}$; Halbach 1970; see Table 2). The l/w relation of the two *Brachionus* species coincided very well (*B. dimidiatus* l : 0.68 ± 0.004 ; *B. plicatilis* l : 0.71 ± 0.006 ; SE, $N=56$). Assuming a density of $\sim 1 \text{ g} \cdot \text{cm}^{-3}$ (Lohmann 1908) and dry weight to be 9% of the wet weight (Ermann 1962), a medium sized *B. plicatilis* ($l=250 \mu\text{m}$) should then weigh 0.27 μgDW . Though volume based DW-estimates are vulnerable to error, the results are consistent with published data: for a *B. calyciflorus* of comparable size Störkel (1977) measured a DW of 0.24 μg and Dumont et al. (1975) 0.25 μg (Dumont's estimate is based on a regression equation relating length to weight).

The volume of eggs was estimated from plasticine models and converted to DW using the same WW/DW relation as for adults. The DW of *Hexarthra jenkiniae* was estimated assuming a cylindrical shape of the rotifer. As *Hexarthra* adds only very little to the rotifer biomass, this rather crude approach seems acceptable. *Cephalodella* did not occur during the period of regular sampling.

For transformations of DW to energy units Störkel's (1977) Figures for *B. calyciflorus* were used: 1 gDW corresponds to 4,654 cal (adults), 5,033 cal (juveniles), 4,772 cal (female + egg) and 4,761 cal (population mean). This is close to 4,640 cal given by Ermann (1962) for an adult *B. calyciflorus* and 4,784 cal given by Walker (1973) for female + egg of *B. plicatilis* (assuming an ash content of 4.6% of the DW; Störkel 1977).

Error estimates. Tests for reproducibility of sampling and counting had a SE of $\pm 6.8\%$ (19 samples at high, 19 at low rotifer densities). The mean SE of the 19 monthly samples was 21%, of lorica length measurements 2.5%, of length-volume-dry weight conversion 10%, and of weight

Table 3. Mean density and biomass of rotifers 1972–1978 (with SE). Numbers of months sampled are indicated in brackets after the year. For biomass figures ♀♀ and eggs of all species were pooled (*B. dimidiatus*, *B. plicatilis*, *H. jenkiniae*). Data of November 1974 to August 1976 are from T. and V. Schwan (pers. comm)

Year	Density, $\text{N} \cdot 10^4 \cdot \text{m}^{-3}$				Biomass		
	<i>B. dimidiatus</i>		<i>B. plicatilis</i>		mgDW $\cdot \text{m}^{-2}$	mgDW $\cdot \text{m}^{-3}$	kJ $\cdot \text{m}^{-3}$
	♀	eggs	♀	eggs			
1972 (8)	222 ± 98	138 ± 60	0	0	160	65 ± 29	1.3
1973 (7)	857 ± 207	349 ± 104	17 ± 11	19 ± 12	570	288 ± 55	5.7
1974 (11)	879 ± 367	313 ± 87	569 ± 256	256 ± 111	2,980	1,843 ± 712	36.7
1975 (9)	1,335 ± 510	469 ± 123	385 ± 178	108 ± 47	2,230	1,389 ± 550	27.7
1976 (8)	2,225 ± 1,303	773 ± 393	156 ± 137	57 ± 49	1,510	1,013 ± 585	20.2
1978 (1)	340	185	0	0	307	96	1.9
1972–1976 (43)	1,102	407	220	86	150	906	18.1

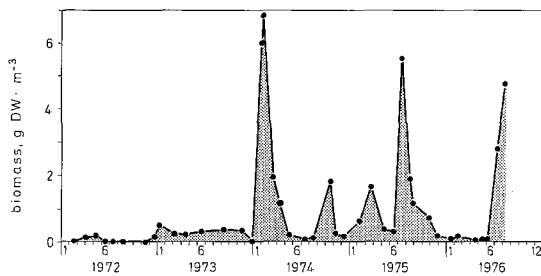


Fig. 4. Mean biomass of rotifers (*Brachionus dimidiatus*, *B. plicatilis*, *Hexarthra jenkiniae*) in 1972–1976; all species pooled (see Fig. 5 for relative percentages of the three species)

energy conversion 3% (Stöckel 1977). The total SE of rotifer biomass estimates was therefore 24.5%.

Results and discussion

Vertical distribution of rotifers was tested by sampling at 2400 h, 0600 h, 1200 h and 1800 h at 6 depths 30 cm apart. No particular pattern was evident, only the early morning samples usually had significantly fewer animals at the deepest point, almost anoxic at that time, and so probably avoided by rotifers.

Horizontal distribution. Rotifer samples taken at the 19 regular sampling points had a mean CV of 91%, indicating high density variations. Rotifer biomass tends to increase towards the shore (Fig. 3). Highest concentrations are along the north and south shores, probably induced by lake currents (the prevailing wind direction is north-south).

Temporal changes. Rotifers had the most irregular pattern of biomass change of all consumer species (Fig. 4). Almost insignificant in 1972 (mean DW 65 mg m^{-3} , Table 3) and still of minor importance in 1973, they increased to considerable densities in 1974 ($1,800 \text{ mg DW} \cdot \text{m}^{-3}$). At the time of the breakdown of the *Spirulina*-bloom in early 1974 (see Fig. 2) they had a peak density of almost $7,000 \text{ mg DW} \cdot \text{m}^{-3}$, which rivals that of the main consumer *Phoeniconaias minor* (mean 1972/73 = $5,280 \text{ mg DW} \cdot \text{m}^{-3}$; peak densities $11,640 \text{ mg DW} \cdot \text{m}^{-3}$); Fig. 5 demonstrates that *B. plicatilis* accounts for most of this rotifer increase. Though little is known about rotifer feeding in saline lakes (Vareschi and Jacobs 1983), it seems likely that a mass development of bacteria by *Spirulina* destruction was responsible for this rotifer bloom. Algal breakdown with parallel mass development of *B. dimidiatus* and *B. plicatilis* also occurred in October 1974, July–September 1975 and July/August 1976 (cf. Fig. 2 and 4).

These data clearly show that rotifers are an important part of the ecosystem. This is further emphasized by their small size and hence high metabolic rate. Data from other tropical lakes usually show much lower densities: e.g. in L. George rotifer numbers fluctuate around $15 \cdot 10^4 \cdot \text{m}^{-3}$ (Burgis et al. 1973), probably contributing <1% to zooplankton biomass. Walker (1973) recorded *B. plicatilis* in densities of $\sim 200 \cdot 10^4 \cdot \text{m}^{-3}$ (maximum $710 \cdot 10^4 \cdot \text{m}^{-3}$) in the saline-alkaline Lake Werowrap (Australia) which is also considerably less than Nakuru numbers for this species (mean 1973–1976 = $362 \cdot 10^4 \cdot \text{m}^{-3}$, maximum *B. plicatilis* $2,103 \cdot 10^4 \cdot \text{m}^{-3}$). The best correspondence with the L.

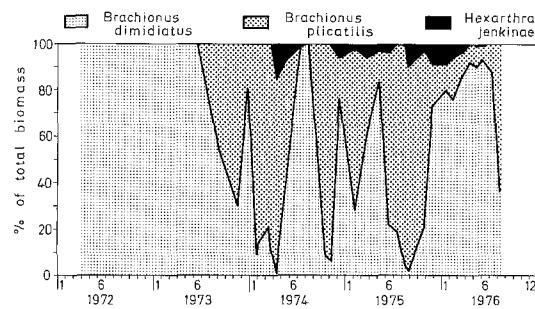


Fig. 5. Numerical percentual contribution of the three species to total rotifer biomass (Fig. 4) 1972–1976

Nakuru data are in the alkaline-saline lakes of Chad (Itlis and Riou-Duwat 1971 and Pourriot and Roungier 1975): *B. dimidiatus* is most abundant (up to $62,000 \cdot 10^4 \cdot \text{m}^{-3}$; Lake Nakuru $34,000 \cdot 10^4 \cdot \text{m}^{-3}$, highest density sampled), followed by *B. plicatilis* (up to $3,600 \cdot 10^4 \cdot \text{m}^{-3}$; L. Nakuru $6,500 \cdot 10^4 \cdot \text{m}^{-3}$) and *H. jenkiniae* (up to $1,000 \cdot 10^4 \cdot \text{m}^{-3}$; L. Nakuru $650 \cdot 10^4 \cdot \text{m}^{-3}$).

The Chad lakes show similar sharp population peaks (*B. dimidiatus* in mare de Latir: from $400 \cdot 10^4 \cdot \text{m}^{-3}$ to $46,000 \cdot 10^4 \cdot \text{m}^{-3}$ within 1 month, January 1966; L. Nakuru: *B. dimidiatus* from $100 \cdot 10^4 \cdot \text{m}^{-3}$ to $3,700 \cdot 10^4 \cdot \text{m}^{-3}$ and *B. plicatilis* from 2 to $2,100 \cdot 10^4 \cdot \text{m}^{-3}$ in January/February 1974). Observations of Williams (1981) in Australian salt lakes suggest that the fluctuations of rotifer densities and species composition observed in L. Nakuru are triggered in part by salinity changes: *H. jenkiniae* occurs in Australian salt lakes in a salinity range of 20–60‰ (~ 18 –55 mS) and *B. plicatilis* in a range of 1–60‰; in L. Nakuru *H. jenkiniae* apparently thrived only at salinities of >20 mS while *B. plicatilis* seems largely impervious to salinity.

3. Aquatic heteroptera

The aquatic heteroptera of L. Nakuru were first identified by Hutchinson (1932) from samples collected in 1929 by the Percy Sladen Expedition to rift valley lakes in Kenya: they consist of the corixids *Micronecta jenkiniae* Hutch., *Micronecta scutellaris* Staal and *Sigara hieroglyphica kili-mandjaronis* Kirk., and of the notonectid *Anisops varia* Fieb. (found in 1929 only in Naivasha Crater Lake [=L. Sonachi]).

Methods

For quantitative heteroptera sampling, a conical lift net was used ($r=0,5 \text{ m}$; $h=1.2 \text{ m}$; mesh size 1.25 mm). Lowered with a 2 m hoist, it was left at the bottom for 1–2 min, and pulled up by hand as fast as possible. The turbidity of the water (Secchi disk reading <15 cm) reduced visibility from 5–10 cm in the upper layers to almost zero at 50 cm (Vareschi 1979), so the water bugs could not avoid the net visually (for error estimates see below). *Micronecta jenkiniae* and some smaller larvae of the two other corixids passed the net, but a finer mesh would have caused too much blockage. Therefore abundance of these small corixids was estimated from vertical hauls of a plankton net ($\varnothing 25 \text{ cm}$, meshsize 300 μ). All water bugs netted were pre-

Table 4. Length and weight of aquatic heteroptera. Length is full length without legs; mean DW of larvae was calculated from DW of the various instars and their mean frequency distribution in representative samples. Corixid measurements are from Mavuti (1975)

	<i>Anisops varia</i>		<i>Micronecta jenkiniae</i>		<i>M. scutellaris</i>		<i>Sigara h. kilimajaronis</i>	
	Larvae	Imagines	Larvae	Imagines	Larvae	Imagines	Larvae	Imagines
Length, mm	2.4–8.0	9.0 (8.5–10)	0.66–2.34	3.6	0.9–3.5	4.5	1.4–3.1	6.1
Mean DW, mg	4.5 (0.8–7.0)	9.9	0.12 (0.004–0.16)	0.28	0.4 (0.04–0.5)	1.2	1.4 (0.04–1.9)	2.8
F × DW = FW	4.7	3.3	8.3	6.0	8.3	6.0	8.3	6.0

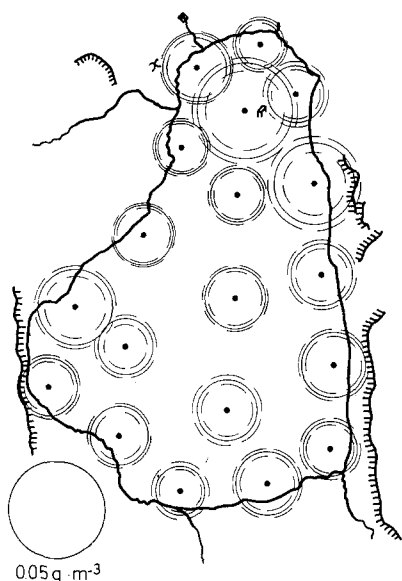


Fig. 6. Mean horizontal distribution of the notonectid *Anisops varia*. See Fig. 1 for explanation

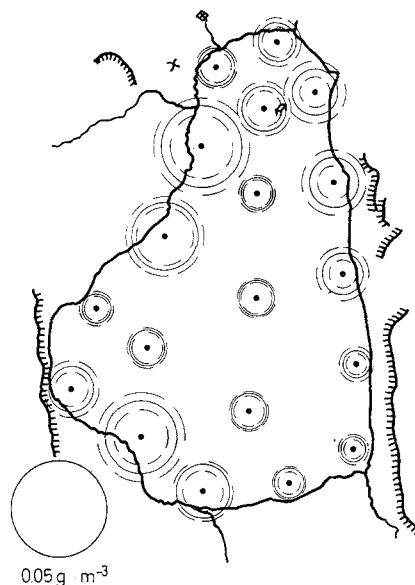


Fig. 7. Mean horizontal distribution of corixids (all three species pooled). See Fig. 1 for explanation

served in formalin for measuring and counting within 24 h of collection. For growth rate experiments the three corixid species were reared at our field station from egg to adults (Mavuti 1975) so that we were able to identify each species at all developmental stages. But to facilitate counting, species were each sorted into only two size classes, juveniles and adults: *M. jenkiniae* < 2.4 mm, 2.4–3.0 mm; *M. scutellaris* < 4.5 mm, 4.5–5.5 mm; *Sigara* < 5.5 mm, 5.5–7.5 mm. As for the notonectid *Anisops*, 3 size classes were distinguished (in mm): 3.5–4.5 (\cong instars I–III), 4.5–7.5 (\cong IV, V) and 7.5–11 (adult). For a length/weight calibration curve larvae and instars (5 stages, $N=30$ per stage) were dried at 85° C for 6 h and weighed (Table 4). For biomass estimates the two *Micronecta* species were lumped. Caloric equivalents were taken from Cummins and Wuycheck (1971). Based on the results of transect samplings average lake biomass was calculated as midlake. 0.6 + inshore. 0.4 (see p. 76 for mode of calculation).

Error estimates. Though it was hardly possible for the water bugs to avoid the lift net visually, it might have been detected with mechanoreceptors. In this case using a bigger net should reduce escape chances and yield higher density estimates. Three different sizes of nets were used for 12 casts within the same region every 15 min. The bigger net, 200 × 200 cm, caught a mean of 332 ± 23 (SE) · m⁻² (*Anisops*

and corixids), the smaller net, 50 × 50 cm, a mean of 317 ± 24 (SE) · m⁻² and the round net, 1 m \varnothing , 321 ± 25 (SE) · m⁻² (SE = 7% of the mean). The differences are not significant, apparently the water bugs were not able to avoid any of the nets. – The SE of both length measurements and of dry weight estimates was 1.5%. – The mean SE of the monthly casts at the 19 sampling stations and the resulting total SE of biomass estimates (in brackets) was 29% (30%) for *Anisops*, 45% (46%) for *Micronecta* and 41% (42%) for *Sigara*.

Results and discussion

Horizontal distribution. Samples taken at the 19 regular sampling points showed a mean CV of 126% (corixids) and 196% (*Anisops*), reflecting a very high variability of horizontal distribution. Comparison of the means (1972–1973) of the 19 stations revealed, however, that most of this variability is not site-specific (Figs. 6 and 7).

Anisops showed a slight but significant preference for inshore areas, but it was always present in considerable numbers at midlake stations (Fig. 6). This pelagic occurrence of *Notonectidae* is quite unusual, normally they are restricted to littoral zones (e.g. *Notonecta glauca* in the shallow Neusiedler See, Austria; Waitzbauer 1967). Corixids showed a marked preference for inshore areas (Fig. 7).

Table 5. Density and biomass of aquatic heteroptera, 1972–1978 (with SE). Numbers after years indicate month of sampling. Larval stages I and II were not counted. Estimates for *Micronecta* include *M. jenkinsae* and *M. scutellaris*

Year	<i>Anisops varia</i>			<i>Micronecta</i>		<i>Sigara</i>	
	Numbers · m ⁻³		Biomass mgDW · m ⁻³	Numbers · m ⁻³		Biomass mgDW · m ⁻³	Biomass mgDW · m ⁻³
	Adults	Juveniles		Adults	Juveniles		
1972 (4–12)	5.7	2.5	24.9 ± 4	3.5	6.4	7.9 ± 2	0.22 ± 0.1
1973 (1–12)	2.9	0.2	13.8 ± 5	2.7	0.9	6.3 ± 5	1.05 ± 0.1
1974–1976 (1–12)	0	0	0	few	few	?	0
1978 (8)	0	0	0	few	few	?	0

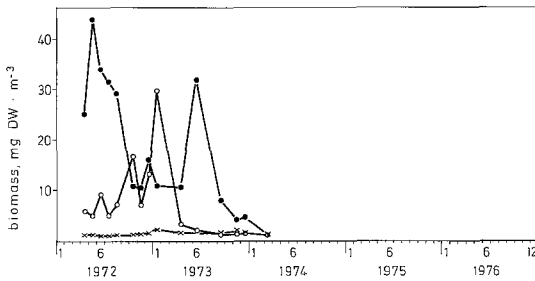


Fig. 8. Biomass of aquatic heteroptera in 1972–1976. Full circles: *Anisops varia*, open circles: *Micronecta scutellaris* and *M. jenkinsae*, crosses *Sigara hieroglyphica kilimanjaronis*. After April 1974 no aquatic heteroptera were in the open water of L. Nakuru

In 1974, when the lake was very low, it was virtually free from aquatic heteroptera. As soon as rising lake levels flooded stands of the rush *Typha domingensis* and the sedge *Cyperus laevigatus* (in late 1974, 1975 and 1976), these areas became densely populated with corixids, but the open lake was never repopulated (up to August 1978).

Temporal changes. Fig. 8 gives temporal changes of heteroptera biomass. *Anisops* had two distinct population peaks (May 1972 and June 1973), Corixids had a peak in January 1973. In March 1974, after the change in ecosystem structure (p. 72), all water bugs except a few *Sigara* had disappeared.

The most likely causes for the observed density fluctuations are changes in salinity and food. Macan (1963) noted corixids as characteristic for saline lakes (up to 80‰ salinity), but Knowles and Williams (1973) reported that they do not occur in south-east Australian lakes with salinities of >15‰. Nakuru corixids showed peak densities when lake conductivity was <16,000 μS ($\approx 14.5\%$), decreasing densities during a conductivity rise up to 22,000 μS ($\approx 20\%$) and virtually no corixids at >23,000 μS ($\approx 21\%$); the small populations occurring at certain shore regions mentioned above might have survived through seepage of freshwater, characteristic for these shore regions. The apparent correlation between conductivity and corixid occurrence in 1972/73 is somewhat questioned by the observations that corixids did not recur when lake conductivities were below 20,000 μS in late 1974 and 1975 and in August 1978 (Fig. 2). However, from 1974 to 1978 the staple food organism of Nakuru corixids, *Spirulina platensis* (Mavuti 1975; Vareschi and Jacobs 1983), was absent or in very low densities. Therefore, the available data suggest that in addition to a substantial influence of conductivity, the lack of *Spirulina* was a limiting factor. The same considerations may also apply to the disappearance of *Anisops varia*: their

main food organism, *Lovenula africana*, also declined early in 1974 (see p. 76). The seeming alternation of corixid and notonectid density peaks (Fig. 8) may hint at a predator-prey-type regulation of their populations, but corixids are probably too small a part of *Anisops*' diet for this (Vareschi and Jacobs 1983).

4. Benthos

The benthic fauna of L. Nakuru is remarkably poor in species: it consists of one and sometimes two chironomid species, *Leptochironomus deribae*¹ and *Tanytarsus horni* (Lake Chad for instance has 47 Chironomids, Dejoux 1968). Nematods were found only very occasionally and the undersides of stones along the western shore were populated by the Coleoptera *Helochaeres spec.* (Hydrophiliidae). Characteristic benthos species of other lakes, e.g. oligochaetes, chaoborides, ostracodes or molluscs are completely absent.

Methods

Benthos samples were obtained with an Ekman-Birge grab taking 0.0225 m², filled into polyethylen bags and stored in a cooling box for 3–20 h. For laboratory processing samples were flushed through a set of 4 sieves (mesh size 10 mm, 5 mm, 1 mm, 300 μ). The residues were searched, all animals counted and measured while still alive and later preserved in formalin.

Rechecking of mud already sieved with an additional sieve (mesh size 125 μ) revealed a loss of 35% of the larvae <2.5 mm long and <5% of bigger stages. Larvae <2.5 mm contributed so little to the total biomass that the considerable effort needed to quantify these stages was not considered worth while. Occasionally the latest larval stages and pupae were found in the plankton hauls. These were added to benthic biomass. For a length/dry weight calibration curve larvae of <2, 2–3, 3–4, ... 7–8 mm length (10–15 of each size) and pupae were dried to weight constancy (~ 12 h, 80°C) and all larvae of one size weighed together with an analytical balance (accuracy 10⁻⁵ g, Fig. 9). As measuring all larvae to 1 mm took too long, the larvae were grouped into size classes of <2.5, 2.5–5, >5 mm and pupae (Fig. 9). Dry weight estimates of benthos samples did not differ significantly whether 1 mm or 2.5 mm size classes were used. All dry weight estimates were therefore based on length measurements for size classes of 2.5 mm and converted to weight using the mean length/

¹ Dejoux (1971) classified this species as *Chironomus (Cryptochironomus) deribae* Freeman 1957, following the opinion of Ringe 1970

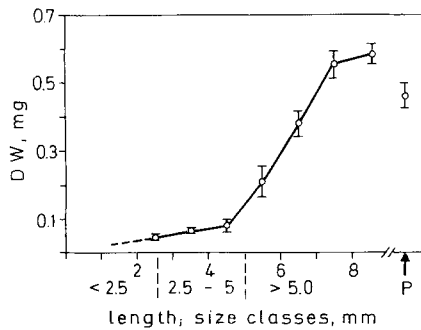


Fig. 9. Length/weight relationship of *Leptochironomus deribae*. For samples of each size ~ 15 larvae were used. P stands for pupae

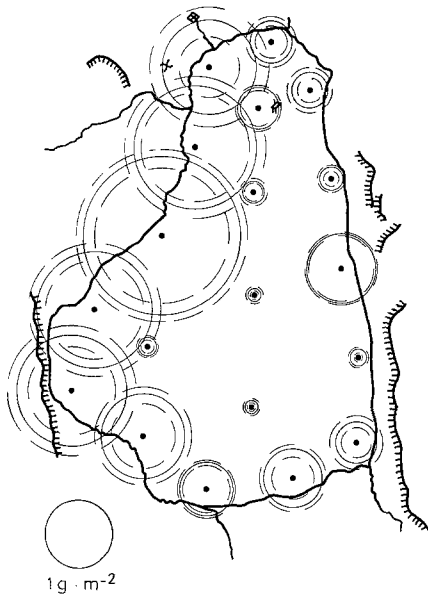


Fig. 10. Mean horizontal distribution of chironomid larvae (*Leptochironomus deribae* and *Tanytarsus horni*), 1972–1976. Highest densities are along the western shore, where sandy sediments dominate

weight relationship given in Fig. 9. The wet-dry weight relation was established by comparing live larvae dried with tissue paper and oven dried larvae: $WW = 7.0 (\pm 0.2, SE) \cdot DW$ ($N=10$; corresponding to a water content of 86%). This agrees well with the factor 6.7 established by Walker (1973). Using calorific values for *Tanytarsus barbicansis* given by Walker (1973), 1 gDW is equivalent to 5,860 cal or 24.5 kJ.

Error estimates. The reproducibility of Ekman samples was tested by taking 12 consecutive grabs in a circle around the anchored boat. The mean of these samples had a SE of $\pm 6.6\%$. Monthly biomass estimates were based on 19 casts, one at each sampling point (Fig. 10). The mean SE of samples at the 19 sampling stations was 31% (inshore areas) and 21% (midlake). Size class classification and DW estimates had a SE of 3%. Therefore the total SE of biomass estimates was roughly 32% (inshore) and 22% (midlake).

Results and discussion

Horizontal distribution. Benthos samples taken at the 19 regular sampling points had a mean CV of 135%, reflecting

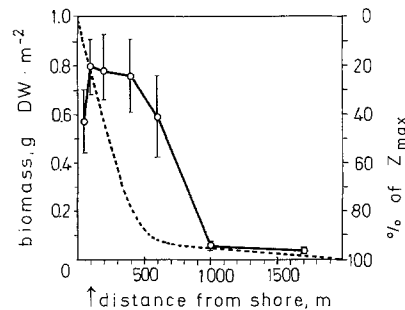


Fig. 11. Horizontal distribution of chironomid-larvae (dry weight with SE; $N=7-14$) in relation to distance from shore. The arrow indicates mean shore distance of the regular sampling points. Broken line: mean lake depth of the sampling points in % of the deepest point (=100%)

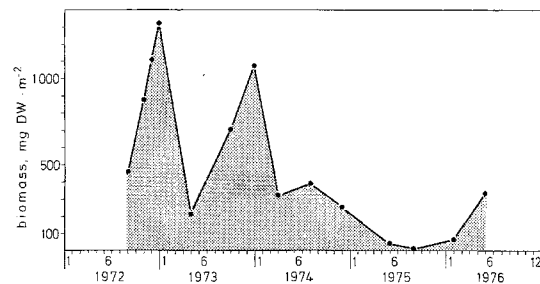


Fig. 12. Mean biomass of chironomid larvae in 1972–1976. Both species (*Leptochironomus deribae* and *Tanytarsus horni*) are pooled

a very uneven distribution of chironomid larvae (Fig. 10). Transect samples in steps of 50, 100, 200, 400, 600 and 1,000 m from the shore at the 14 shore sampling points and samples at the 5 midlake points (mean distance from shore = 1,700 m; Fig. 11) permit an assessment of inshore to midlake gradients of chironomid larvae biomass. Fig. 11 shows that the biomass of larvae increased from the shore to 100–400 m, followed by a steep decrease of 90% towards midlake. Mean biomass in 1972–1976 was $86 \pm 15 \text{ mgDW} \cdot \text{m}^{-2}$ (midlake) and $1,100 \pm 420 \text{ mgDW}$ (inshore). The 14 inshore sampling points revealed a characteristic distribution pattern (Fig. 10): the larvae concentrated along the western shore which accounts for $\sim 80\%$ of the lake's benthos biomass (points 8–13; highest mean biomass at point 11: $5,300 \text{ mgDW} \cdot \text{m}^{-2}$). Sediments along the western shore are often sandy while deep organic ooze dominates the eastern shore and midlake. The unstable nature of this soft mud may be unfavourable for chironomid larvae (Darlington 1977). In the South African lake St. Lucias Boltz (1975) found a similar distribution of chironomid larvae: $1.08-3.26 \text{ gDW} \cdot \text{m}^{-2}$ on sandy and $0.013-0.063 \text{ gDW} \cdot \text{m}^{-2}$ on muddy substrates. Boltz's observation confirms that the horizontal benthos distribution of L. Nakuru is probably determined by the type of sediments prevailing. But in L. George (Uganda) Darlington (1977) found only a slight preference for inshore areas (midlake $250 \text{ mgDW} \cdot \text{m}^{-2}$; inshore $420 \text{ mgDW} \cdot \text{m}^{-2}$), though sediments also tend to be more soft and unstable in midlake.

Temporal changes. As the 14 inshore points of regular sampling coincided with maximum larvae biomass, it was necessary to weigh figures according to station positions to derive an estimate of mean lake biomass. From a graphic represen-

Table 6. Mean density and biomass (with SE) of chironomid larvae (*Leptochironomus deribae* and *Tanytarsus horni*), 1972–1978. Numbers after the years indicate months of sampling; 2 to 3 samples per year in 1974–1976. Midlake stations had a mean shore distance of 1,700 m, inshore station ~200 m. Data for 1975 and 1976 are from T. and V. Schwan (pers. comm)

Year	Midlake		Inshore		Whole lake		
	N·m ⁻²	gDW·m ⁻²	N·m ⁻²	gDW·m ⁻²	N·m ⁻²	gDW·m ⁻²	kJ·m ⁻²
1972 (8, 10, 11, 12)	404	0.10±0.03	12,615	2.09±0.40	4,137	0.94±0.18	23.1
1973 (4, 9, 12)	467	0.07±0.03	7,033	1.49±0.55	3,240	0.67±0.25	16.4
1974–1976	442	0.08±0.03	2,501	0.37±0.11	1,316	0.20±0.06	4.9
1978 (8)	430	0.08	6,520	1.31	2,990	0.60	14.7
Mean 1972–1976	427	0.086	6,022	1.10	2,534	0.60	14.8

tation (Fig. 11) of the data the following equation was derived: mean lake biomass = mean inshore biomass · 0.42 + mean midlake biomass · 0.58. Table 6 and Fig. 12 give mean density and biomass estimates for the years 1972–1976. From April 1972 to August 1973 only *L. deribae* occurred, but from September 1973 to November 1974 *T. horni* came up in very low numbers (approx. 1% of chironomid biomass), increasing to 5% in May 1974 and 56% in January 1976. Until 1974 temporal biomass changes seem to follow a regular pattern with peak densities in the dry season (November–March) and lowest densities during the rains in April and May. Inshore samples accounted for most of the observed population changes, midlake samples retained their levels (Table 6). Highest densities were reached in December 1972 and 1973: $6,950 \pm 2,370 \cdot \text{m}^{-2}$ ($\pm 1.32 \pm 0.45 \text{ gDW} \cdot \text{m}^{-2}$) and $5,190 \pm 1,950 \cdot \text{m}^{-2}$ ($\pm 1.08 \pm 0.4 \text{ gDW} \cdot \text{m}^{-2}$) respectively. At sampling station 11 (Fig. 10) peak densities were $47,700 \cdot \text{m}^{-2}$ ($\pm 11.7 \text{ gDW} \cdot \text{m}^{-2}$) $\pm 48 \text{ gWW} \cdot \text{m}^{-2}$, 1973; the number/weight relationships indicate that in 1973 smaller sizes prevailed. 1974–1976 show a completely different pattern with no seasonal variations. The difference between the patterns 1972/73 and 1974–1976 coincides with a different ecosystem structure of the lake (p. 72). For a causal analysis of chironomid larvae population dynamics considerably more data would be needed.

T. horni seems to be halophilic: it appeared at L. Nakuru only when salinities were high and it is the only chironomid of Lake Bogoria (=L. Hannington), an alkaline rift valley lake of 70–90‰ salinity.

Chironomid biomass of L. Nakuru exceeds L. George values but it corresponds to the total benthos biomass of L. George (midlake 0.98 ± 0.12 , inshore $1.13 \pm 0.24 \text{ gDW} \cdot \text{m}^{-2}$, Darlington 1977; excluding benthic *Chaoborus*), it is within the lower range cited by Rawson (1930) for 110 northern hemisphere lakes (0.7 – $16 \text{ gDW} \cdot \text{m}^{-2}$) and well below estimates of Paterson and Walker (1974) for an Australian salt lake (L. Werowrap; mean 8.1; max. $15.9 \text{ gDW} \cdot \text{m}^{-2}$) and $8.5 \text{ gDW} \cdot \text{m}^{-2}$ reported by Cole (1968) for richest lakes of North America. However, one should keep in mind that biomass figures at temperate lakes are usually summer values, whereas mean annual biomass is given for tropical lakes.

5. Birds and hippopotamus

In contrast to the very low species diversity in the lake, the surroundings have a very rich wildlife and especially birdlife: Schmidl (pers. comm) lists 433 bird species of which

119 depend on the lake or tributaries as a food source and 40 of them are fish eaters. As fish were introduced only about 20 years ago these birds are a fairly new addition to the ecosystem. Their feeding and excreta could have a noticeable impact on the lake. Some observations on the main fish-eating birds and a few others are therefore included in this study.

Methods

Regular bird and Hippopotamus counts were made from the boat while moving from one sampling point to the next observing with binoculars (see appendix). Each observation was recorded with a portable tape recorder. The huge aggregations of the Great White Pelican *Pelecanus onocrotalus* (up to 2,800 birds within one flock) were estimated by counting sections of the flock and judging the number of similar sections. Three counts in March 1974 were done with the help of 12 groups of volunteers, each group counting the birds along an approx. 2 km shore section. Greater Flamingos were counted three times by binocular observations from the shore, and also from aerial pictures if the photographic quality allowed distinction between Greater and Lesser Flamingos. Most fish-eating birds tended to stay near the lake on mud flats and beds of sand with very little vegetation, cormorants, darters and some egrets preferred certain stands of acacia trees near the shore as roosting or nesting places. Though these circumstances facilitate bird counting, some will of course be missed and all counts tend to be underestimates. Pelicans breeding on L. Elmenteita were counted from aerial photographs. Individual bird weights were taken from published data (see footnotes, appendix).

Results and discussion

The results of all bird censuses from October 1972 to October 1974 are given in the appendix, together with aerial counts of Lesser Flamingos for comparison. Fig. 13 gives biomass estimates 1971–1974.

Fisheating birds. The Great White Pelican (*Pelecanus onocrotalus*) dominates overwhelmingly, accounting for >90% of the biomass of fisheating birds. Pelican numbers increased steadily from low levels to peak densities of 20,400 in October 1974 (=254 metric tons WW; if not stated otherwise, all biomass figures in this chapter relate to the whole lake). At this time apparently most of the Rift Valley population of about 22,000 birds (in 1968/69; Bartholomew

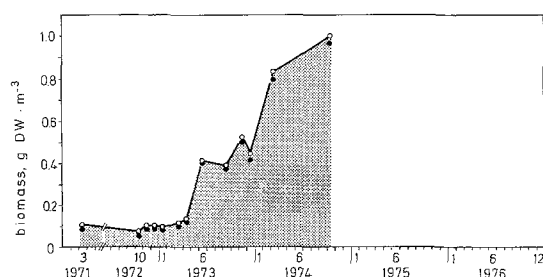


Fig. 13. Biomass of fish-eating birds, 1971–1974 (open circles) and biomass of Great White Pelicans (*Pelecanus onocrotatus*), closed circles. Data for March 1971 are from Hopcraft 1971

and Pennycuik 1973) was concentrated at L. Nakuru. By the end of 1974 their numbers declined again to about the level of 1971/72 (Mburugu, pers. comm.); they had possibly exhausted their food supply at L. Nakuru (Vareschi and Jacobs 1983). Since 1968, that is about 8 years after fish were introduced into L. Nakuru, *P. onocrotatus* has bred regularly at L. Elmenteita, a fishless alkaline-saline lake 14 km from L. Nakuru (Brown et al. 1973, reported a total of 8,000 breeding pairs, raising some 7,000 young birds between July 1968 and January 1971). In 1968 and in 1973/74 the pelican population and the breeding colony were among the largest ever reported for African lakes, and pelican density (birds/km shore line) considerably exceeded estimates for other lakes (Din and Eltringham 1973; Bartholomew and Pennycuik 1973; Berry et al. 1973). – In 1976–1978 Brown (pers. comm.) recorded several large-scale breeding attempts at L. Elmenteita, but with far less success than in 1973/74: in 1976 2–3,000 pairs were breeding; in 1977 8,000 breeding pairs abandoned their hatching young because of water rising above the nests and in 1978 3,000 pairs lost their young for the same reason.

Second in biomass of fish-eating birds is the White-necked Cormorant (*Phalacrocorax carbo*; mean biomass 1972–1973 ~850 kg, max. ≈4,050 kg, WW). It breeds regularly at L. Nakuru, concentrating in a large colony at the north-west corner of the lake: in August 1973 and June 1974 almost all suitable trees around the lake were occupied. The Little Grebe (*Poliocephalus ruficollis*) sometimes attains very high numbers and considerable biomass (~400 kg, WW), but countings of these small and well-camouflaged birds are difficult and were too infrequent to give a fair estimate. Of the remaining fish-eating birds only the Pink-backed Pelican (*Pelecanus rufescens*) and the Yellow-billed Stork (*Ibis ibis*) come up to a biomass of ~200 kg (WW), the other 34 fish-eating species are of only marginal importance.

Non-fish-eating birds. Greater Flamingos (*Phoenicopterus ruber roseus*) usually number only 1–5% of the Lesser Flamingos. Brown et al. (1973) estimated the whole Rift Valley population as 50,000 birds, about 20% of these at L. Nakuru. *P. ruber* share the Elmenteita breeding sites with *P.*

onocrotatus: Brown et al. (1973) counted 10 breeding attempts from 1951–1971, involving a total of ~65,000 adult birds and resulting in ~10,000 young reared to fledging. The decline of Greater Flamingo numbers in early 1974 could be related to the disappearance of copepods: copepods and benthic organisms seem to be the staple foods of Greater Flamingos, as indicated by stomach analysis: it contained almost entirely copepods in 1972, copepods, some chironomid larvae and detritus in 1973 and only chironomid larvae and detritus in 1974. The Fish Eagle population (*Haliaeetus vocifer*) has only one or two breeding pairs, a very low number for East African lakes (Brown and Cade 1972, Brown and Hopcraft 1973). Fish Eagles were never observed to prey on fish at L. Nakuru: the water is too turbid to allow visual preying and fish are rather small (mean length ~5 cm, maximal length ~20 cm): Fish Eagles switched to flamingo feeding. Marabou Storcks (*Leptoptilus crumeniferus*) are much more abundant in comparison to other lakes. Essentially scavengers, they also changed to flamingo preying: they can kill healthy adults by drowning or breaking the neck, but usually they prefer infirm birds. Other birds of prey are too rare to have any quantitative impact on the lake. Mammals known to prey on flamingoes (jackal, hyaena) were never observed to do so at L. Nakuru.

Hippopotamus. The hippopotamus (*Hippopotamus amphibius*) could have considerable impact on the lake as a nutrient importer: at night it feeds on shore but during the day stays in the lake and defecates accordingly. Therefore hippopotamuses were also counted from the boat during the bird counts (see appendix), resulting in about 15 animals (including 3–5 immatures).

Conclusions

A biotope of spatial homogeneity but temporal discontinuity, with a few species dominating the flora and fauna, characterizes Lake Nakuru as a relatively simple ecosystem.

In 1972/73 only three species contributed overwhelmingly to the mean total consumer biomass (10.0 gDW · m⁻³): *Phoeniconaias minor* (53%), *Sarotherodon a. grahami* (24%) and *Lovenula africana* (15%). Although after 1973 total consumer biomass (9.0 gDW · m⁻³ in 1974) resembled the preceding years, the relative importance of some consumer organisms had changed (e.g. rotifers compensated for the loss of copepods). For the following years (1975, 1976 and 1978) data are insufficient to allow a telling comparison.

In tropical Africa two lakes comparable to L. Nakuru have been thoroughly investigated: L. George, Uganda (see Burgis et al. 1973, for data and references) and the three ecological regions of L. Chad, Chad (see Carmouze et al. 1972, for data and references); both lakes are as shallow as L. Nakuru but they are larger and less saline (see Table below). Looking at different consumer groups, the mean zooplankton biomass in 1972 and 1973 is considerably higher than comparable estimates for L. George (including 50%

	\bar{z} (m)	Area (km ²)	Conductivity (μS , 20° C)	Zooplankton (gDW · m ⁻³)	Fish (gDW · m ⁻³)	Benthos (gDW · m ⁻²)	Σ consumer (gDW · m ⁻³)
L. Nakuru (1972; 1973)	1.5–3.1	~40	~20,000	1.9; 1.5	0.9; 3.9	1.0; 0.8	8.6; 11.4
L. George	2.4	250	200	0.61	2.3	1.0	3.9
L. Chad	2–4	20,000	50–1,500	0.26	0.4–3.9	0.4–6.5	1.1–10.6

Appendix

Bird counts and hippopotamus numbers of L. Nakuru; the birds are arranged by their contribution to total bird biomass. For details of counting methods see p. 78; Lesser Flamingo numbers are from aerial counts (Vareschi 1978). Weights (= wet weights) are from Brown and Urban (1969) and Brown et al. (1982). The bird count of March 1971 is from Hopcraft (1972)

Species	Weight per indiv. (g)	1971		1972					1973					1974					1978	
		Mar	1971	Oct	Nov	Dec	Jan	Mar	Apr	Jun	Sep	Nov	Dec	20-3	23-3	27-3	29-3	Oct	Aug	
Lesser Flamingo (Phoeniconaias minor)	1,800	-	858 · 10 ³	-	-	762 · 10 ³	474 · 10 ³	501 · 10 ³	900 · 10 ³	818 · 10 ³	-	1,137 · 10 ³	1,082 · 10 ³	-	-	-	-	172 · 10 ³	~100 · 10 ³	
Great White Pelican (Pelecanus oncorotatus)	11,300	3,000	1,730	2,525	2,630	2,290	2,500	2,850	4,305	4,100	6,930	4,645	7,245	5,990	5,880	8,440	20,440	3,500	3,500	
Breeding G.W. Pelicans L. Elmenteita, ad., young	-	-	0	0	0	0	0	0	4,500	-	-	4,000	-	-	-	6,100	300	0	0	
Cormorants ^a	2,100	1,000	1,460	1,250	790	1,550	1,040	1,215	995	-	1,630	-	2,475	1,975	1,425	1,775	1,925	1,800	1,800	
Cormorant nests ^b	-	-	420	370	-	-	320	320	410	507	620	-	-	180	-	-	-	>300	-	
Little Grebe (Polioccephalus ruficollis) ^c	200	5,000	5,000	5,000	5,000	5,000	5,000	5,000	5,000	5,000	8,000	8,000	8,000	8,000	8,000	8,000	8,000	5,000	2,315	
Yellow Billed Stork (Ibis ibis)	4,000	240	175	250	140	40	75	130	150	105	50	80	110	264	150	102	460	210	210	
Pink-backed Pelican (Pelecanus refescens)	5,400	-	150	55	42	9	103	88	110	107	216	160	450	-	-	-	-	-	-	
Spoonbill (Platales alba)	1,500	170	110	150	160	125	140	60	35	70	80	130	104	190	100	160	12	40	40	
Large Egrets and Herons ^d	2,000	100	80	50	30	25	40	45	30	30	70	30	30	100	120	100	110	130	130	
Darter (Anhinga anhinga)	2,000	-	90	138	101	19	21	45	13	4	0	0	0	0	0	0	0	0	few	
Tern (Chlidonias leucoptera)	70	1,960	few	1,000	1,000	1,000	2,000	few	few	few	2,000	3,000	3,000	3,000	3,000	3,000	500	-	-	
Small Egrets and Herons ^e	600	100	25	35	15	20	50	10	20	15	10	60	20	50	80	30	90	39	39	
Greater Flamingo (Phoenicopterus ruber)	3,000	-	5,000	5,000	5,000	5,000	5,000	7,000	10,000	25,000	20,000	10,000	1,100	730	840	715	760	~1,000	~1,000	

Bird counts and hippopotamus numbers of L. Nakuru; the birds are arranged by their contribution to total bird biomass. For details of counting methods see p. 78; Lesser Flamingo numbers are from aerial counts (Vareschi 1978). Weights (= wet weights) are from Brown and Urban (1969) and Brown et al. (1982). The bird count of March 1971 is from Hopcraft (1972)

Species	Weight per indiv. (g)	1971			1972			1973			1974			1978						
		Mar	Apr	May	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept				
African Fish Eagle (<i>Haliaeetus vocifer</i>)	2,800	-	-	-	18	22	24	21	16	13	20	5	21	8	41	16	3	20	12	5
Marabou Stork (<i>Lepotiflus crumeniferus</i>)	5,500	-	-	-	45	45	75	75	170	100	105	175	50	95	140	130	120	100	180	24
Hippopotamus (<i>Hippopotamus amphibius</i>)	3.5 · 10 ⁶	-	-	-	12	6	10	17	18	19	16	15	13	6	2	-	-	-	16	6

^a White Necked Cormorant (*Phalacrocorax carbo*) and Long Tailed Cormorant (*P. africanus*)

^b Only nests outside the main colony were counted during bird counts; to this figure the ~300 nests of the main colony were added ("Home of Cormorants" near Park Gate); in June and August 1974 and March and June 1974 the main colony was counted as well; only nests with breeding activity were included. Cormorant nests listed under September 1973 were counted in August 1973 (W. Sudhaus, pers. comm.); a further census in June 1974 resulted in 510 nests with a mean of 2.5 young birds per nest

^c Not counted individually, only a very rough estimate from several random samples (1972-1976)

^d Great White Egret (*Casmerus albus*); Yellow Billed Egret (*Mesophoxys intermedias*); Black Headed Heron (*Ardea melanocephala*); Grey Heron (*Ardea cinerea*) and others

^e Little Egret (*Egretta garzetta*); Cattle Egret (*Bubulcus ibis*); Night Heron (*Nycticorax nycticorax*); Squacco Heron (*Ardeola ralloides*) and others

of the biomass of the half planktonic, half benthic *Chaoborus* larvae) and L. Chad. Mean ichthyomass is within the same range in all three lakes. The mean benthic biomass of 1972 and 1973 (almost exclusively chironomid larvae) is within the range of L. George (*Chaoborus*, chironomid larvae and oligochaetes) and somewhat lower than of Chad (main biomass due to molluscs). But the total consumer biomass of L. Nakuru (including birds) is much higher than values for L. George and L. Chad; it is also higher than most estimates of summer maxima for temperate lakes (see Kajak and Hillbricht-Ilkowska 1972 for data and references).

Compared with other tropical lakes the consumer biomass of L. Nakuru shows some peculiarities: In L. Nakuru a bird (the Lesser Flamingo) generally dominates consumer biomass (59%), whereas in most tropical and temperate lakes invertebrates are the dominant consumers (in some tropical lakes also fish, e.g. L. George: 59% of the consumer biomass). In L. Nakuru benthic organisms contribute only 4% to total consumer biomass, considerably less than in most other tropical lakes (e.g. L. George 25%, L. Chad 58%). In L. Nakuru most food chains have two links only and the most important predators forming the second consumer level live outside the water (Greater Flamingos and pelicans), whereas in most other lakes food chains have in general at least three links and the highest predators are generally fish.

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