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Population structure and secondary productivity of *Limnodrilus hoffmeisteri* (Claparede) and *Branchiura sowerbyi* Beddard in the profundal zone of Lake Naivasha, Kenya

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Abstract

Lake Naivasha has been well studied since the 1930s but attempts to understand its ecological functioning have had to wait until enough was known about its structure. The energetics of the lake has only been studied to date at primary producer level. Following the identification of the invertebrate components of the littoral and profundal benthos, this study was initiated. The absence of native fish species in Lake Naivasha, combined with a fishery based only on three, introduced species, added an applied dimension to the work. The introduction of additional fish species which will utilize unexploited ecological niches has been suggested. The benthic invertebrates form one such niche. Two oligochaetes dominated the community, *Branchiura sowerbyi* Beddard and *Limnodrilus hoffmeisteri* Claparade. The former had a productivity of 7.4 g m^{-2} ann^{-1} (as dry weight), the latter 0.6. These figures are not particularly high and do not support the introduction of a new fish species on their own.

Introduction

There is a paucity of fish species in Lake Naivasha, with only one native species, believed to have become extinct in the 1960s and five exotic species introduced between 1926 and 1965 (Harper et al., 1990; Hickley et al., this volume). The cause is believed to be the instability of the inflows, which led to the lake becoming dry for much of the 19th Century (Becht & Harper, 2002). The importance of the lake as a commercial fishery since 1959, based on these few species, led Mavuti (1990) to recommend introduction of zooplanktivorous, commercially important fish to exploit uncropped zooplankton because no fish permanently occupy the limnetic zone leading to zooplankton production directly entering the decomposer food chain. Hickley et al. (2002) recommend a benthic-feeding fish such as *Mormyrus* spp. because no benthivore was present. It was known that the benthic invertebrates consisted of two oligochaetes – *Limnodrilus hoffmeisteri* Claparade and *Branchiura sowerbyi* Beddard – together with several species of chironomids with the former predominating in abundance (Clarke et al., 1989).

A knowledge of the life cycle of tubificids is a precursor to the determination of their secondary production. Taxonomic problems, however, have led to scarcity of data on many life cycles. *L. hoffmeisteri* is one of the most widespread and abundant tubificid species in the world (Kennedy, 1965). The life cycle of this species has received appreciable attention in temperate regions (Kennedy, 1966; Ladle, 1971; Aston, 1973; Poddubnaya, 1980) but not in the tropics. Success in establishing the life cycle of *L. hoffmeisteri* has largely been facilitated by culturing the worms in the laboratory (Kennedy, 1966; Aston, 1973). Information on the life cycle of *B. sowerbyi* on the other hand is scarce (Carrol & Dorris, 1972). An account has been given by Casellato (1984), based on cultured populations.

This study focused on the life cycle and production of these two tubificids, *L. hoffmeisteri* and *B. sowerbyi* as the former is the most numerically abundant species while the latter contributes the highest benthic biomass in Lake Naivasha (Raburu, 1991). The specific objectives of the study were to establish the population structure and to estimate the productivity of the two species.

Study area and methods

Lake Naivasha at an altitude of 1890 m a.s.l. is the highest and largest freshwater lake of the Eastern Rift Valley of Kenya. The lake is located at latitude 0 °45′ and longitude 36° 20′ E. The main lake (150 km^2) is a more or less circular, endorrheic, basin while two other water bodies, Crescent Island lagoon and Oloidien lake (5.5 km^2) are connected at high water levels, separate at low. Crescent Island lagoon is the deepest part of the lake. The main lake was the only basin sampled in this study as this is the focus of the commercial fishery.

Monthly sampling of the macrobenthos was carried out along four transects off the eastern shore (Safariland SL), the southern (Hippo Point HP), the western (Mennell's Lagoon ML), and the northern (North Swamp (NS), from September, 1989, to August, 1990. Each transect had five sampling stations 500 m apart (Fig. 1). Grab samples were taken in triplicate at each sampling station with a 15 × 15 cm Ekman grab which closes by means of a messenger. The top was covered with a fine (335 μm) stainless steel gauge to prevent animals in the top few centimeters of sediment from escaping as the grab penetrates the soft bottom substrates.

The macro-invertebrates were sieved from the sediment through a 0.3 mm mesh sieve. Sorting was carried out by hand on fresh samples when organisms had their natural colours and were mobile, which contributed to quicker and more efficient sorting. After sieving they were identified, counted and weighed and their lengths measured while still alive, before preservation in 4% formaldehyde. In Naivasha, *L. hofmeisteri* does not occur in association with any other species of the genus *Limnodrilus* and it was presumed that all immature specimens belonged to the same species (Clark et al., 1989).

The fresh weight was recorded when specimens were still alive. After sorting into different species, excess water was removed by placing them onto a filter paper. The weight was recorded to the nearest 0.01 g using an electronic balance. Biomass determinations were derived from dry weight but, since the same specimens whose wet weights were taken (especially *L. hoffmeisteri*) had to be mounted on slides for further analysis, a conversion factor was established from the regression of dry weight on wet weight (Ladle, 1971; Gieve, 1975) of 50 samples of tubificid worms collected from the lake. The dry weight of the worms was obtained by drying them to a constant weight in a vacuum at 60 °C for 36 h.

The population structure of *L. hoffmeisteri* was established by grouping the worms into two categories. These were (a) immature individuals not possessing a penis tube on the 9th segment and (b) mature individuals possessing penis tube on the 9th segment (Brinkhurst, 1966). Other workers (Kennedy, 1966; Aston, 1973) managed to group *L. Hoffmeisteri* into immature, breeding and mature worms. This was not possible in this study because immature and breeding worms are not easy to distinguish either by chaetal characteristics or presence of spermatophores (Ladle, 1971). Classification of *L. hoffmeisteri* is further complicated by the fact that sexually mature worms resorb the penis tube after reproduction (Kennedy, 1966; Ladle, 1971; Aston, 1973; Poddubnaya, 1980) and revert to an immature condition which cannot be differentiated from a truly juvenile worm. In this study, the width of the 9th segment which contains the penis tube was used as an index of size obviating problems with breakage. Worms were mounted in dimethyl hydantin formaldehyde (DMHF) under 22 × 50 cm coverslips. After clearing for 2 days, the worms were observed under a compound microscope (magnification 24×) to locate and measure the width of the 9th segment using a graduated micrometer eyepiece. Worms were grouped into size classes 0.11–0.16, 0.17–0.21, 0.22–0.26, 0.27–0.31, 0.32–0.36, 0.38–0.42, 0.43–0.47 and 0.48–0.52 mm.

The weight of worms in each size class was calculated from the equation obtained from the relationship between the width of the 9th segment and the mass of *L. hoffmeisteri* in different size classes: weight = 0.0239 + 0.161 width.

The number of *B. sowerbyi* cocoons in grab samples were counted every month from September, 1989 to August, 1990. From May to October 1990, the lengths of live *B. sowerbyi* were measured to the nearest 0.1 mm. This was done by placing the worms in a wet groove drilled in the middle of a plastic ruler and the length taken when the worms were relaxed. They were grouped into four length classes: 0.1–3.0cm, 3.1–6.0 cm, 6.1–9.0cm and 9.1–12+ cm. Monthly variation in the number of cocoons and length frequency of *B. sowerbyi* were recorded. The

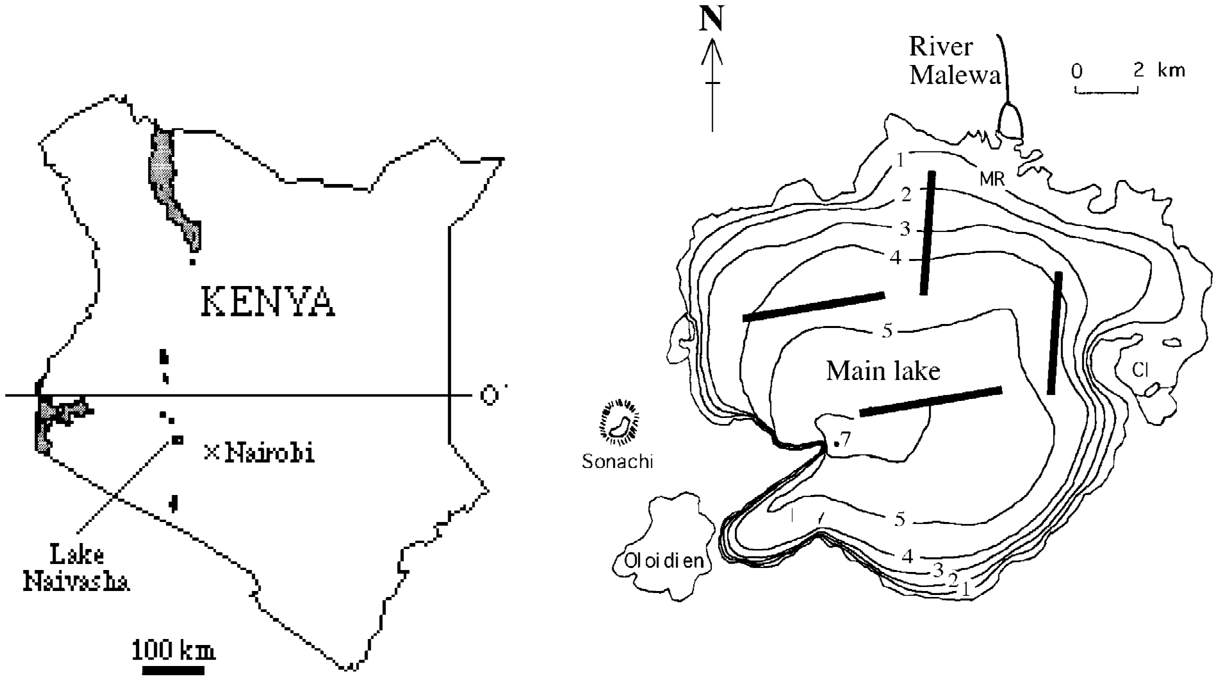

Figure 1. Location of sample transects in Lake Naivasha.

worms in each size class were counted and weighed alive using an electronic balance to the nearest 0.01 gram. Dry weights of tubificid worms could not be obtained on every sampling occasion because worms were mounted for further analysis. A conversion factor was therefore established from the regression of the dry weight on wet weight of both species:

$$\text{Dry weight} = 0.005 + 0.17705\ (\pm 0.0041),$$
$$\text{wet weight}\ (r = 0.987,\ P < 0.05).$$

The regression coefficient gave the percentage dry weight of wet weight to be 17.7%.

The first two size classes of *L. hoffmeisteri* (0.11–0.16 and 0.17–0.21 mm) were excluded in the production estimate as they were under represented probably due to the mesh size of sieve used. Productivity of *L. hoffmeisteri* and *B. sowerbyi* were estimated using a modification of Hynes method to give a direct estimate of the number of individuals growing into a particular size category (Nj) (Hynes & Coleman, 1968; Menzie, 1980). The equations used were:

$$N_j = in_j \times \text{Pe/Pa} \times 365/\text{CPI},$$

where i = the size categories into which the organisms are placed; Pe = estimated proportion of life cycle spent in a particular length class; Pa = the actual proportion of life cycle spent in a particular length class; n = the mean number of individuals in the size class; CPI = the cohort production interval in days from hatching to attainment of the largest aquatic size.

N_j is then substituted into the equation estimate production:

$$\text{P} = (N_j - N_{j+1}) \times (W_j W_{j+1})^{1/2},$$

where P = the annual production (g dry weight/m^2/yr). W_j = the mean weight of an individual in the *j*th size category (g). $(W_j W_j + 1)^{1/2}$ = the geometric mean weight between two size classes (g).

Results

The total annual mean benthic biomass of all macroinvertebrates was 4.07 g dry weight m^{-2} with *Branchiura sowerbyi* accounting for about 58% (2.37 g dry weight m^{-2}), *L. hoffmeisteri*, 27% (1.10 g dry weight m^{-2}). Chironomids made up 8% and other oligochaetes and microturbellarian worms, respectively, 4% and 3% (Raburu, 1991).

Immature worms dominated the population of *L. hoffmeisteri* throughout 12 months (Fig. 2). The lowest proportion of immature in the population composed (57%) occurred in October 1989, a month when the mature worms were breeding. The proportion of immature worms in the population of *L. hoffmeisteri* in

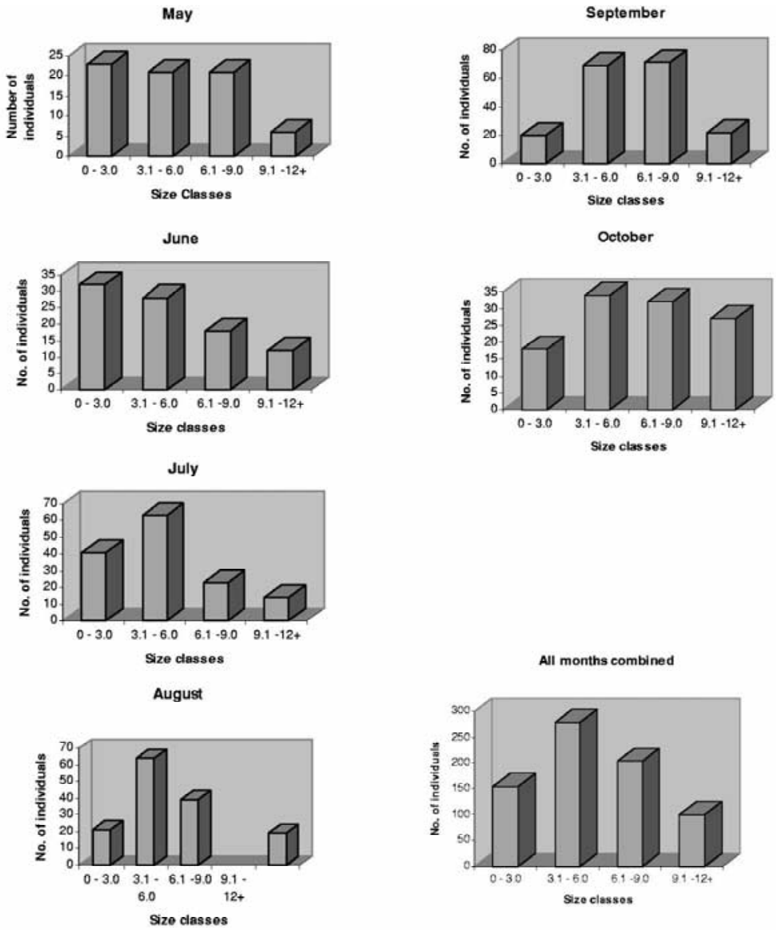

Figure 2. Abundance of *Limnodrilus hoffmeisteri* in Lake Naivasha

the lake then increased consistently from November 1989 to July 1990 when the ratio of immature to mature worms was 17:3. Reproduction of *L. hoffmeisteri* in Lake Naivasha was thus continuous with a peak in October. The smallest size-class was low throughout the study period, probably indicating insufficient collection. Size class 0.22–0.26 mm was most numerous from September 1989 to January 1990, 0.27–0.31 mm in February and March 1990 and 0.22–0.26 mm again from April to August 1990. When monthly observations on the width of the 9th segment of *L. hoffmeisteri* were pooled, the 0.22–0.26 mm size-class had the highest number of individuals followed by the 0.27–0.31 mm and 0.17–0.26 size-classes.

Cocoons of *B. sowerbyi* occurred throughout the study (Fig. 3), indicating continuous breeding, more abundant between January and March reaching a peak in March dropping therafter. Variation in length frequencies of *B. sowerbyi* from May 1990 to October 1990 shows the population was dominated by juvenile worms throughout the year, unlike *L. hoffmeisteri*, where, there was a progression in abundance from one size group to the next.

Productivity

The annual productivity of *L. hoffmeisteri* is shown in Table 1. Since there is one peak in cocoon production a year, the time taken by a young worm to develop to the largest aquatic size was assumed to be one year (CPI). Time taken by the worms to grow from one size class to the next was assumed to be one month. From these assumptions, the parameters Pe/Pa and 365/CPI, were 1.5 and 1.0, respectively. The annual productivity of *L. hoffmeisteri* was 0.65 g dry weight m^{-2} ann^{-1} and the annual production to mean biomass ratio (P/B) of 8 per year.

Table 2 shows that the calculation of the productivity of *B. sowerbyi* was 7.43 g dry weight m^{-2} ann^{-1}

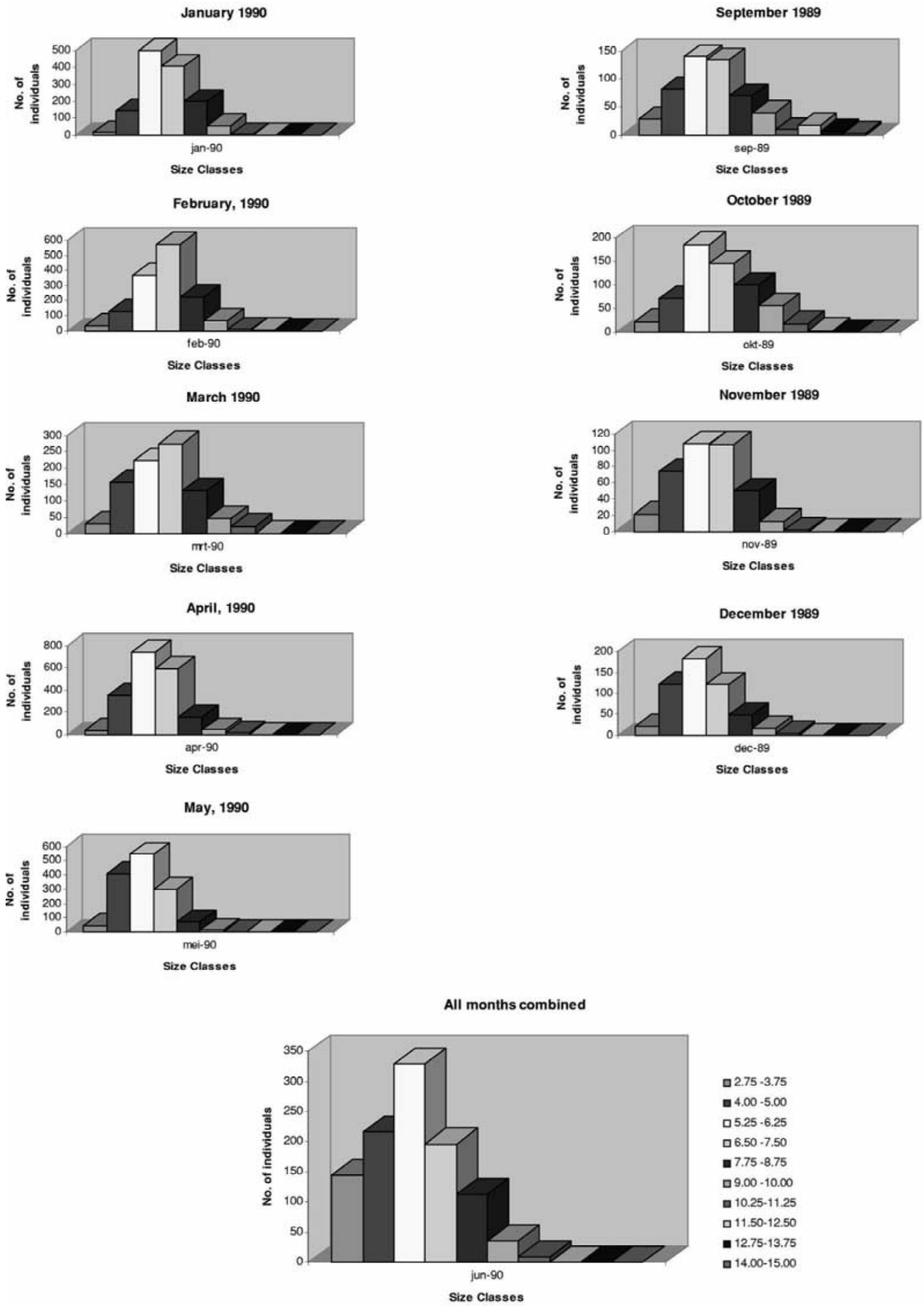

Figure 3. Abundance of *Brachiura sowerbi* in Lake Naivasha

Table 1. The secondary production of *L. hoffmeisteri* by Hynes' method. Column 1 is the total number of worms/m^{-2}, 2 is the mean number of individuals in the size-class, 3 is the mean weight of an individuals in the size category, 4 is biomass, 5 is the number of individuals that develop into a particular size category during the year, 6 is the number of individuals lost between successive size category, 7 is the geometric mean weight between two size classes, 8 is the production

Size group Width (mm)	1 N No m^{-2}	2 $\bar{n}$ n	3 Wj (g)	4 B (g m^{-2})	5 Nj	6 (Nj−Nj+1)	7 (WjWj+1)− (g)	8 (Nj−Nj+1)×(WjWj+1)− g dry wt m^{-2}yr^{-1}
0.11–0.16	549	46	8.17×10^{-5}	0.045	552	−1788	4.36×10^{-5}	(−0.078)
0.17–0.21	2338	195	2.33×10^{-5}	0.054	2340	−1560	1.76×10^{-5}	(−0.028)
0.22–0.26	4684	390	1.35×10^{-5}	0.062	4680	660	1.54×10^{-5}	0.010
0.27–0.31	4015	335	1.76×10^{-5}	0.070	4020	2472	3.00×10^{-5}	0.074
0.32–0.36	1543	129	5.10×10^{-5}	0.079	1548	1080	9.79×10^{-5}	0.106
0.38–0.42	471	39	1.88×10^{-4}	0.088	468	336	3.79×10^{4}	0.127
0.43–0.47	126	11	7.65×10^{-4}	0.096	132	108	1.95×10^{3}	0.211
0.48–0.52	21	2	4.97×10^{-3}	0.104	24	24	4.97×10^{-3}	0.119
			BB = 0.08				TOTAL	= 0.647

Table 2. The secondary production of *B. sowerbyi* by Hynes' method. Column 1 is the total number of worms m^{-2}, 2 is the mean number of individuals in the size-class, 3 is the mean weight of an individuals in the size category, 4 is biomass, 5 is the number of individuals that develop into a particular size category during the year, 6 is the number of individuals lost between successive size category, 7 is the geometric mean weight between two size classes, 8 is the production

Size group Lengths (cm)	1 2 no m^{-2}	2 $\bar{n}$ n	3 Wj (g)	4 B (g m^{-2})	5 Nj	6 (Nj−Nj+1)	7 (WjWj+1)− (g)	8 (Nj−Nj+1)×(WjWj+1)− g dry wt - m^{-2}yr^{-1}
0.1–3.0	155	26	2.067×10^{-3}	0.32	138	−138	0.0041	(−0.566)
3.1–6.0	274	46	8.012×10^{-3}	2.20	276	66	0.0089	0.587
6.1–9.0	210	35	9.991×10^{-3}	2.10	210	108	0.0130	1.404
9.1–12+	100	17	1.691×10^{-2}	1.69	102	102	0.0169	1.724
			B = 4.79				TOTAL	= 3.715 × 2
								= 7.43

B = Mean biomass.

and a P/B ratio of 5. In the calculation of productivity of *B. sowerbyi*, Pe/Pa and 365/CPI values used were 0.5 and 1.0, respectively. The worms were assumed to develop to the largest aquatic size in 1 year and they took 2 months to grow from one size class to the next.

The total production of dominating tubificid oligochaetes *B. sowerbyi* and *L. hoffmeisteri* is therefore 8.08 g dry weight m^{-2} ann^{-1}.

Discussion

Comparing the biomass of benthic macroinvertebrate communities in shallow tropical African lakes is not easy due to scanty data on benthic biomass, seasonally or over a number of years. It often depends on the dominating species, which are usually either oligochaetes, dipteran larvae (*Chaoborus* or chironomid) or molluscs. In Lake Chad, the mean benthic biomass for the whole lake was 3.7 g dry weight m^{-2} being dominated by molluscs (Leveque et al., 1983). In Lake George, a very low mean benthic biomass of 0.74 g dry weight m^{-2} was recorded during the dry seasons (Burgis et al., 1973), which rose during wet periods to 9.76 g dry weight m^{-2} in the mid-lake area and 11.31 g dry weight m^{-2} inshore (Darlington, 1977). The dominant species were dipteran larvae (*Chaoborus* and chironomids). In Lake Chilwa, a shallow endorrheic lake with levels experiencing annual fluctuations, the mean benthic biomass during the 1967 dry season was 0.07 g dry weight m^{-2} and was dominated by chironomids (McLachlan & McLachlan, 1969). In Lake McIlwaine, Zimbabwe, Munro (1966) estimated that

Table 3. Biomass and benthic production in other lakes compared with Lake Naivasha

Lake	Biomass ($g\ m^{-2}$ dry weight)	Productivity ($g\ m^{-2}$ dry wt ann^{-1})	Dominant taxa	Author(s)
Chad 13° N	3.7	–	Molluscs and Insects	Leveque et al. (1983)
	0.257	14.76	Total Molluscs	"
	0.126	–	Total Oligochaete	"
	3.503	–	Total Insecta	"
George 0°	1.2	–	*Chaoborus* and Chironomids	Burgis et al. (1973)
	0.74	–	" " "	Darlington, (1977)
Chilwa 15° S	0.07–0.32	–	Chironomids, Coleoptera and Diptera	McLachlan & McLachlan (1969)
McIlwaine 17° S	3	–	Insects and Oligochaetes	Munro (1966)
	5.0	–	Chironomids	Marshall (1978)
	18.8	–	Oligochaete	"
Kariba	0.02–0.1	–	Chironomids	McLachlan & McLachlan (1969)
Sibaya 27° S	2.1235	0.1534 $g\ m^{-2}d^{-1}$	*Grandidierella lignorum*	
	3.6158	0.281 $g\ m^{-2}d^{-1}$	*Apseudus digitalis* & *Potamon Sidneyi* (2 month study)	Hart (1979)
Naivasha 0° 45′ S	1.095	0.65	*L. hoffmeisteri*	Present study
	2.365	7.43	*B. sowerbyi*	"
Leman (France)		3.33	*L. hoffmeisteri*	Lafont (1987)
Rybinsk Reservoir (Russia)		6–43 (wet weight)	*L. hoffmeisteri*	Poddubnaya (1980)
Donghu (China)		5.7–33.5 (wet weight)	*B. sowerbyi*	Liang (1984)
Sierra Nevada Peatlands		58–74 (wet weight)	Oligochaeta	Erman & Erman (1975)
Lake Esrom (Denmark)	16.5	92.6 Kcal m^{-2} ann^{-1}	Chironomids and *Chaoborus* sp.	Jonasson (1972)
		1.5 " "	*Ilyodrilus hammoniensis*	
		6	*Pisidium casertanum*	

the benthic biomass was 3 g dry weight m^{-2} at a time when the benthos was dominated by insects and oligochaetes. Later, Marshall (1978) found the mean benthic biomass of chironomids and oligochaetes to be 5.0 and 18.8 g dry weight/m^2, respectively, which are extremely high values compared to other African lakes.

Lake Naivasha is morphometrically similar to Lakes Mcllwaine, Chad, Chilwa, and George. The benthic biomass in the profundal region of Lake Naivasha falls within the range recorded in other African lakes with higher standing crop than many lakes. In both Lake Naivasha and Lake Mcllwaine, the tubificid *B. sowerbyi* contributes about 60% of profundal benthic biomass.

Data on benthic productivity is almost non-existent in African lakes except for Lakes Sibaya and Chad. The productivity of *Caridina nilotica* in Lake Sibaya was 37.5 g dry weight m^{-2} ann^{-1} (Hart, 1979) while the productivity of the entire molluscan assemblage was 14.76 g dry weight m^{-2} ann^{-1} in Lake Chad (Leveque et al., 1983). In Lake Naivasha, the productivity, considering the kind of species studied, was high (Table 3).

Secondary production in benthic communities is normally limited by habitat complexity, biological interactions, temperature and the quantity and quality of food (Benke, 1984). The relative importance among these factors differs among different benthic environments and in their influence on different species in any given community. According to Butler (1982), major factors limiting production of a species are often the same as those limiting life cycle patterns. Temperature does not limit standing stock biomass (Morgan et al., 1980) since high biomasses can be found in very cold and in warm environments. However, it can influence biomass turnover in an environment where there is no stress and abundant food supply (Benke, 1984). In Lake Naivasha, temporal variation in sediment temperature was minimal compared to that in temperate lakes with distinct seasonal fluctuations. Production of benthic communities is therefore unlikely to be limited by temperature. Biological effects (such as competition and predation) on the production dynamics of benthic species is often very complex, and the information about it is scarce (Morgan et al., 1980). The biomass and turnover rates can be limited by the quality and quantity of food. In Lake Naivasha, life cycle patterns and biomass peaks were synchronized with seasonality of rainfall normally associated with injection of fresh food from allochthonous and autochthonous nutrient inputs stimulating primary productivity of phytoplankton. Quality and quantity of food therefore appears to be the major factor limiting the production of benthic macroinverterbrates in Lake Naivasha.

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