8. The benthic fauna: ecology, biomass and communities

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Benthos consists of all those aquatic organisms which are associated in some way with the bottom sediments. We shall, therefore, consider here only the organisms and communities inhabiting the lake sediments, reserving a study of the periphyton found on higher aquatic plants for a further chapter. This periphyton was far from negligible in Lake Chad where fringing vegetation and submerged water grasses were numerous. It was usually composed of different species to the benthos although some were occasionally found among the benthos when it was sampled close to plant clumps.

Most of the observations on the benthic communities and their biomasses were made between 1968 and 1971, i.e. during the 'Normal Chad' period, and a general zonation was established for the Lake in 1970 (Carmouze et al. 1972). The distribution patterns obtained at this time were completely changed later, because of the rapid drop in the Lake level after 1972, which caused partial drought in some zones and major changes in the ecological conditions. The evolution of the benthic communities could only be partly studied during this drying phase of Lake Chad.

All samples were taken with an Ekman grab. For worms and insects, five samples were taken at each station with a 15 × 15 cm grab. The samples, washed on a 0.3 mm mesh sieve, were then fixed in 10% formol, and later sorted in the laboratory. At least six samples were collected for molluscs at each station, with a 30 × 30 cm grab, these washed on a 0.8 mm mesh sieve.

8.1 Composition of the benthic fauna

The bulk of the benthic fauna of Lake Chad was represented by three groups of macroinvertebrates — worms, molluscs insects — which have been the subject of intensive study during recent years.

We give here a list of the most common benthic species. More detailed systematic studies have been published by Dejoux (1968, 1969, 1970, 1971, 1973) for insects, Lauzanne (1968) for oligochaetes, and Lévêque (1968, 1974) for molluscs.

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OLIGOCHAETES

Alluroïdae
Alluroïdes tanganykae
Tubificidae
Aulodrilus remex, Euilodrilus sp.
Naïdidae
Branchiodrilus cleistochaeta, Allonais paraguayensis ghanensis, Pristina synclites, Naïs sp.

Only Alluroïdidae and Tubificidae were abundant in the bottom substrata, while Naïdidae were found only occasionally, for they preferred the water grasses.

MOLLUSCS

Prosobranchia
Melania tuberculata, Bellamya unicolor, Cleopatra bulimoïdes
Lamellibranchia
Corbicula africana, Caelatura aegyptiaca, Caelatura terestiuscula, Pisidium pirothi, Eupera parasitica, Mutela dubia, Mutela rostrata

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The three species of Prosobranchs, as well as *C. africana* and *C. aegyptiaca*, were very abundant with a wide dspribution. The other species were less numerous and more localized.

INSECTS

Chironomids
Chironominae
Chironomus formosipennis, Cryptochironomus stilifer, Cryptochironomus nudiforceps, Cryptochironomus dawulfianus, Cryptochironomus diceras, Tanytarsus nigrocinctus, Polypedilum fuscipenne, Polydepilum griseoguttatum, Polypedilum abyssiniae, Polypedilum longicrus, Cladotanytarsus lewisi, Cladotanytarsus pseudomancus
Tanypodinae
Ablabesmyia pictipes, Ablabesmyia dusoleili, Clinotanypus claripennis, Procladius brevipetiolatus
Orthocladiinae
Cricotopus scottae
Ephemeroptera
Cloeon fraudulentum, Eatonica schoutedeni, Coenomedes brevipes, Povilla adusta
Trichoptera
Dipseudopsis capensis, Ecnomus dispar, Ecnomus sp.

Most of the species in these different invertebrate groups are widely distributed in Africa and none was endemic to Lake Chad.

8.2 Factors influencing species distribution and abundance

Temporal and spatial distribution of benthic organisms depends on various physical and chemical factors which favour or discourage the presence and abundance of species. Other phenomena, such as fish predation, can also play an important role, but none of these processes have been evaluated in Lake Chad so far.

It is true that a number of ecological factors are more or less interrelated. The nature of the sediment, which serves as a universal basis for distinguishing benthic population, results in fact, from a complex group of physico-chemical factors which have not all been identified.

Under these circumstances it is often difficult to determine precisely which factors exercise a real influence on benthic species. It is generally considered sufficient to establish the correlation existing between the density of the species and certain environmental parameters, without confirming the direct relationship that exists between them. Only experimental studies can prove this.

In the case of Lake Chad, we have been able to define the role played by the sediment type, conductivity and temperature on the composition of the communities and the abundance of species. The generally very shallow depth and sufficient oxygenation at the bottom due to thorough mixing by fairly strong winds throughout the year, did not appear to limit the distribution of the benthic fauna as in deeper lakes. However, local vegetation barriers surrounding the islands acted as screens, attenuating the action of the dominant winds, and promoting the formation of swarms of chironomids with a gregarious tendency. The larvae of these chironomids were therefore more numerous near the shores than at the centre, but this phenomenon was relatively infrequent (Dejoux 1976).

8.2.1 *Bottom types*

Granulometry and the chemical characteristics of the sediment are known to play a very important role in the distribution of species and the composition of benthic communities. The influence of these factors has been well studied in Lake Chad (Dejoux et al. 1971; Dupont and Lévêque 1968; Carmouze et al., 1972).

In the region of Bol (southeastern archipelago), which may be considered relatively homogeneous as regards other factors affecting the distribution of species (salinity, type of landscape, etc.), a precise map of the bottom was established by core sampling and by dredging the zone under study. This represented a water surface of about 20 km^2 and mineralogical analyses revealed five characteristic sediment types: sand mud, peat, soft clay and granular clay. Samples from January 1967, at various points in this zone, showed the influence of sediment type on the qualitative and quantitative composition of the malacological communities (Dupont and Lévêque 1968). This study was repeated in January 1970 for the entire benthic fauna (Dejoux et al. 1971). An analysis of variance showed that the 'bottom type' factor was highly significant for most of the worm and mollusc species, but that more than half of the insect larvae were unaffected by it. The factor under consideration was significant for three species only: *Cladotanytarsus lewisi, Polypedilum* sp. III and *Nilodorum rugosum*. The insects therefore were less dependent on a particular sediment than worms and molluscs. It will be noted that the greatest densities of worms and molluscs were to be found on clay bottoms, and those of insects on sandy bottoms (Table 1). Worms and insects were particularly scarce in peat.

Throughout Lake Chad, the bottom features also proved to be important in the distribution of species, although results were not always so clear as at Bol, due to interference from other ecological factors. If the mean densities and biomasses of the principal groups of worms are examined in the four types of bottoms sampled during March and November 1970 (Table 2), it can be seen that the Alluroïdidae were absent from mud, whereas the Tubificidae were abundant there. *Alluroides* was dominant in the 'pseudo-sand', whereas in peat there were no worms. These results confirmed the observations made in the Bol region, with sand being considered of the same texture and granulometry as 'pseudo-sand'. For molluscs the phenomenon was less clear, for it seemed that other factors in relation to geography also had a strong influence. However, in a particular zone, the type of community depended also on the nature of the sediment (Lévêque 1972). Finally for the insects, the results obtained for the whole lake were not comparable with those of the Bol region and other distribution factors probably intervened to a greater extent (Dejoux 1976).

8.2.2 *Conductivity of the water*

The ratio varied from 1 to 15 between the Shari delta and the north of the lake (Carmouze et al., 1972).

A fairly radical change was noticed in the structure of the oligochaete communities on clay beds of about 420 µS cm^{-1}. The Alluroididae, which had the greatest biomass below this threshold, disappeared completely beyond it and were replaced by Tubificidae which became very abundant. An ecological barrier related to the saltiness of the water seemed to exist for *Alluroides tanganyikae*, since this species disappeared from the clay sediments of Lake Chad when conductivity was over 420 µS cm^{-1} (Fig. 1).

An identical phenomenon was observed in the molluscs as the mean density of different species of prosobranchs diminished rapidly from 400 µS. *Cleopatra* and *Bellamya* disappeared above 550 µS and *Melania* beyond 600 µS (Fig. 2). Benthic molluscs were totally absent in samples from the north of the lake, where conductivities reached 750 µS, whereas environmental conditions of sediment, depth and landscape were apparently the same as for water with a lower conductivity. Moreover, in the zone devoid of molluscs, there were many

Table 1 Mean number of individuals (m^{-2}) of the different species of benthic invertebrates for each type of sediment in the Bol region in January 1970 (after Dejoux et al. 1971).

	Soft clay	Granular clay	Sand	Mud	Peat
INSECTS					
Ecnomus dispar	3.0	32.6	14.8		7.4
Cloeon fraudulentum	35.6	213.3	17.8		14.8
Povilla adusta		5.9			
Eatonica schoutedeni		3.0		1.8	
Orthotrichia	5.9	5.9	8.9		
Chaoborus ceratopogones	5.9	5.9			
Ceratopogonides	14.8			5.3	
Ablabesmyia dusoleili	3.0	41.5		16.0	55.6
Chironomus formisipennis	14.8	32.6	3.0	8.9	
Chironomus sp. I	17.8	3.0			
Cladotanytarsus lewisi			962.9		
Cladotanytarsus sp. I	3.0				
Clinotanypus claripennis		3.0		16.0	
Cryptochironomus stilifer	477.0	130.3	23.7	446.2	185.1
Cryptochironomus diceras	11.8	35.5	53.3	1.8	25.9
Cryptochironomus sp. I	5.9	14.8	26.7		
Cryptochironomus sp. II		8.9	204.4		
Cryptochironomus sp. III			11.9		
Cryptochironomus sp. IV					
Nilodorum rugosum	100.7	5.9			
Polypedilum fuscipenne	50.3		29.6	46.2	37.0
Polypedilum sp. I	23.7	5.9		3.6	11.1
Polypedilum sp. II	5.3				
Polypedilum sp. III			405.9		
Procladius brevipetiolatus		5.9			
Stictochironomus sp. I		3.0			
Stictochironomus sp. II		14.8			22.2
Tanytarsus nigrocinctus	3.0	11.8		3.6	
Tanytarsus sp. I	34.9	47.9			32.6
WORMS					
Aulodrilus remex		115.6	231.1	851.0	3.0
Euilyodrilus sp.	32.4	68.0	38.2	11.1	
Alluroïdes tanganikae	1434.0	1431.0	44.4		5.8
Branchiodrilus cleistochaeta	23.6	17.8	8.9	4.4	
Pristina synclites		35.6			
Naïs sp.			414.6		

Table 1 (continued).

	Soft clay	Granular clay	Sand	Mud	Peat
Aulophorus sp.			14.7		5.8
Nématodes	787.9	408.8	85.8	15.6	
MOLLUSCS					
Melania tuberculata	0.3	1.1	8.9	18.5	6.6
Cleopatra bulimoïdes	48.1	222.4	10.2	3.2	24.9
Bellamya unicolor	0.7	2.5	0.5	0.6	0.2
Corbicula africana	5.4	15.4	0.8	0.8	0.4
Caelatura aegyptiaca	1.6	3.1	0.5	0.1	0.1
Pisidium pirothi	0.1	0	0	0	0.1
Eupera parasitica	0.1	11.1	0	0	0

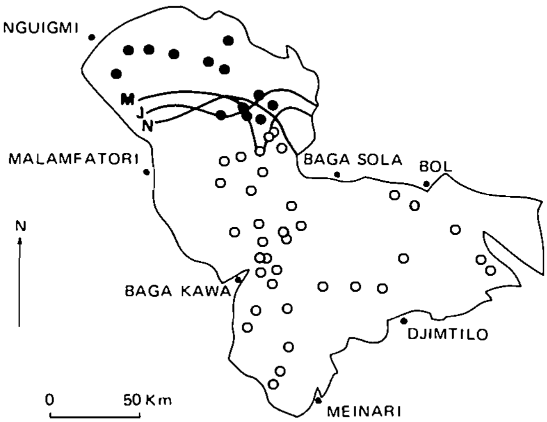

Fig. 1 Worms: distribution of Alluroïdidae on clay substrata (○ = presence; ● = absence). Lines M, J, N indicate the 420 µS cm^{-1} conductivity limits in March, July and November, 1970 (after Carmouze et al. 1972).

dead shells of *Melania* and *Bellamya*, indicating that these species must have prospered there. Finally, we never observed benthic molluscs in the ponds of Kanem with conductivities of 800 to 1000 µS, whereas Pulmonates were present in the vegetation.

The conductivity of the water did not appear to be a limiting factor in the distribution of numerous species of Chironomids (Dejoux 1976). Some of them however seemed to show a preference for high salinities (*Chironomus calipterus,*

Table 2 Mean densities and biomass for each group of benthic worms, according to the main substratum types investigated in March and November 1970 over the whole of the Lake Chad (after Carmouze et al. 1972).

March 1970		Alluroididae	Tubificidae	Naididae	Nématodes	Total
Mud	N m^{-2}	0	9134	54	229	9417
(20 stations)	mg m^{-2}	0	3197	19	14	3230
Clay	N m^{-2}	157	2462	0	1916	4535
(22 stations)	mg m^{-2}	535	866	0	119	1520
Pseudo-sand	N m^{-2}	626	219	30	177	1052
(8 stations)	mg m^{-2}	2132	77	10	11	2230
Peat						
(5 stations)		0	0	0	0	

November 1970		Alluroididae	Tubificidae	Naididae	Nématodes	Total
Mud	N m^{-2}	0	1089	2	70	1161
(22 stations)	mg m^{-2}	0	381	—	4	385
Clay	N m^{-2}	216	540	4	211	971
(27 stations)	mg m^{-2}	736	189	1	13	939
Pseudo-sand	N m^{-2}	369	61	0	50	480
(6 stations)	mg m^{-2}	1257	21	0	3	1281
Peat						
(2 stations)		0	0	0	0	0

Dicrotendipes polosimanus, *Dicrotendipes fusconotatus*, *Tanytarsus nigrocintus*, *Cladotanytarsus lewisi*, *Cryptochironomus diceras*, *Cryptochironomus stilifer*, *Polypedilum laterale*). Others were abundant especially in water with a low salinity (*Chironomus pulcher*, *Chrironomus acuminatus*, *Dicrotendipes peryngeyanus*, *Tanytarsus zariae*, *Tanytarsus flexibile*, *Nilodorum brevipalpis*, *Nilodorum fractilobus*, *Cryptochironomus miligenus*, *Cryptochironomus sinatus*, *Cryptochironomus melutensis*, *Polypedilum longicrus*, *Clinotanypus rugosus*, *Ablabesmyia nilotica*). Finally, in the Kanem ponds or in polders that were drying up, *Cryptochironomus deribae* was abundant, usually associated with *Chironomus calipterus*. *C. deribae*, known in the lagoons of the Camargue and the Baltic, may be considered a very halophilic species.

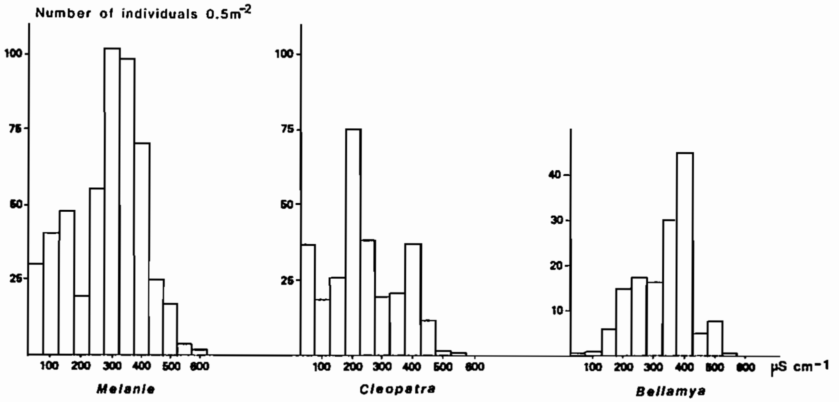

Fig. 2 Relationship between conductivity (µS cm^{-1}) and the mean density per sample for the three species of benthic Prosobranchs in Lake Chad (after Lévêque 1972).

8.2.3 *Seasonal abundance rhythms*

Monthly samples were taken between 1966 and 1967 at twelve stations within the eastern archipelago (Dejoux et al. 1969), and they revealed the existence of a seasonal abundance cycle in worms and insects, related to certain environmental factors. If the yearly change in water temperature and the lake level is compared with that of the mean density and biomass of organisms in the stations studied (Fig. 3), abundance was at a maximum for oligochaetes and insect larvae in the cool season (January to March) when the lake water was high. The minimum was found in the hot season (August to September) at the time of low water. The abundance of these two groups increased with lake level, but fell when the temperature of the water rose during the annual cycle.

The existence of a seasonal abundance rhythm has also been confirmed during missions undertaken over the whole lake in March, July and November, 1970. The greatest densities of oligochaetes (Carmouze et al. 1972) were observed in March, with the lowest in July (Table 4). This was also the case for the insects (Dejoux 1976) (Table 3).

Variation in seasonal abundance could not be shown for molluscs, with the exception of *Corbicula africana*, which reproduced in the cold season, and so had its maximum density (Dejoux et al. 1969; Lévêque 1972).

The low density of benthic organisms at the lowest water level could have been due to the greater disturbance of the sediments with decreasing depth when the wind stirred up the water, making conditions unsuitable for the establishment of dense communities. The tornadoes which occurred from April to June must have also altered the state of the bottom. Finally, the water reached its lowest level in the hot season when the biological cycles of the insects were much shorter than in the cool season.

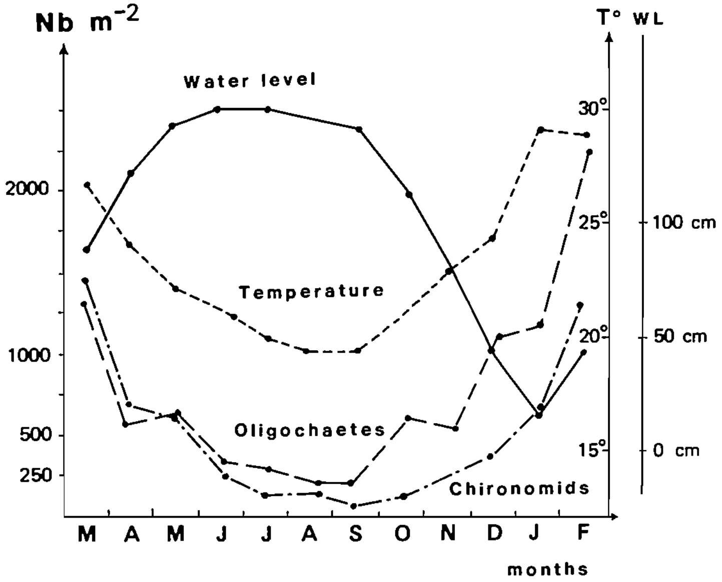

Fig. 3 Variation in mean density of benthic chironomids and oligochaetes for eastern Lake Chad in 1966–1967, with the temperature (T°) and water level (H) on the Bol gauge (after Dejoux et al. 1969, and Dejoux 1976).

Table 3 Variations in mean seasonal density of benthic insect larvae in numbers m^{-2} for three regions of Lake Chad: zone 1, north of the lake, above the Malamfatori parallel; zone 2, center of the lake between the preceding zone and the Great Barrier; zone 3, south and east of the lake (Dejoux 1976).

Date	Zone 1	Zone 2	Zone 3
March 1970	1574	482	369
July 1970	97	27	17
November 1970	540	298	119
March 1971	763	386	47

8.3 Communities and the major ecological zones

Samples from 1968 and 1970 from the whole lake revealed the main community types existing in each group studied. From these data it has been possible to distinguish according to each group, ecological zones within which the communities showed certain similarities regarding specific structure and species density (Carmouze et al. 1972). These main ecological zones clearly emphasized the original character of the different parts of the lake.

8.3.1 *Worms*

Four main ecological zones (Fig. 4) were determined, according to nature of the bottom and conductivity, the principal factors of species distribution. The mean densities and biomass of the worms in the diverse bottom types were calculated in each of these zones (Table 4).

Zone 1 — Open water of the north, consisting mainly of muddy substrate in a 180–420 µS cm^{-1} conductivity range. This zone was rich in Tubificidae which constituted almost the total community.

Zone 2 — Open water of the south and southeast in which the beds were made up of clay and 'pseudo-sand'. Here, the conductivity was below 180 µS, and Alluroididae largely dominated the biomass.

Zone 3 — Archipelago and reed islands of the north, where the conductivity was higher than 420 µS, Alluroïdidae were absent and Tubificidae represented 99% of the biomass in this zone.

Zone 4 — Archipelago and reed islands of the 'Great Barrier' and of the east. The sediments were more varied in this region and the communities were fairly heterogeneous. Tubificidae were found in the mud, whereas the Alluroïdidae were abundant in the clay bottoms.

8.3.2 *Molluscs*

The results of sampling the whole of the lake during 1968 and 1970 defined twenty-five biotopes (Fig. 5) according to three criteria: nature of the bottom, type region (open water, archipelago, reed island) and geographical position

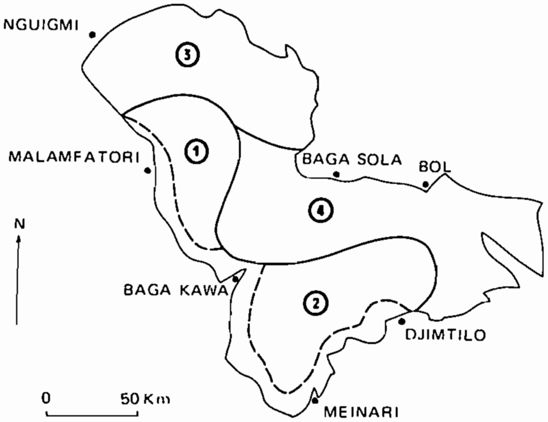

Fig. 4 Main community distribution zones of worms (after Carmouze et al. 1972).

Table 4 Mean densities and biomass of benthic worms in March, July and November, 1970, on the main substratum types and in the four large distribution zones defined for this group (Fig. 4) (after Carmouze et al. 1972).

March 1970		Zone 1	Zone 2	Zone 3	Zone 4
Mud	N m^{-2}	14353		2874	5009
	kg ha^{-1}	50.25		9.97	17.52
Clay	N m^{-2}	2583	500	5867	1083
	kg ha^{-1}	5.23	5.67	20.08	12.45
Pseudo-sand	N m^{-2}		1052		
	kg ha^{-1}		22.30		
Peat	N m^{-2}			0	0
	kg ha^{-1}			0	0

July 1970		Zone 1	Zone 2	Zone 3	Zone 4
Mud	N m^{-2}	279		0	0
	kg ha^{-1}	0.67		0	0
Clay	N m^{-2}		235	0	683
	kg ha^{-1}		6.45	0	8.61
Pseudo-sand	N m^{-2}		808		
	kg ha^{-1}		10.76		
Peat	N m^{-2}			0	0
	kg ha^{-1}			0	0

November 1970		Zone 1	Zone 2	Zone 3	Zone 4
Mud	N m^{-2}	2828		218	412
	kg ha^{-1}	9.44		0.75	0.70
Clay	N m^{-2}	1131	581	4750	372
	kg ha^{-1}	11.51	15.11	15.81	5.39
Pseudo-sand	N m^{-2}		526		
	kg ha^{-1}		12.83		
Peat	N m^{-2}			0	0
	kg ha^{-1}			0	0

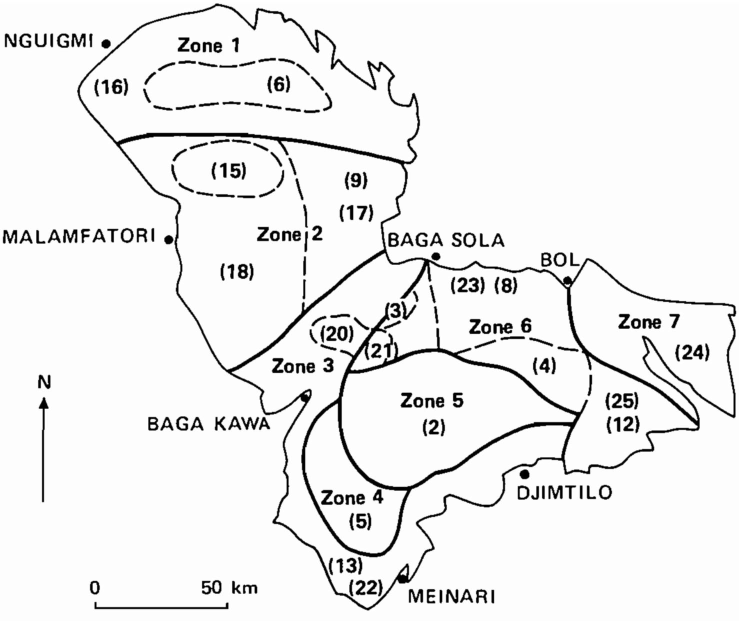

Fig. 5 Localization of the major geographical zones and main biotopes chosen for a study of benthic mollusc communities (after Lévêque 1972); 1 = sand (whole lake); 2 = pseudo-sand (west of the delta); 3 = pseudo-sand of the Great Barrier; 4 = blue clay (east); 5 = granular clay of the south; 6 = granular clay of the north; 7 = granular clay of the Great Barrier; 8 = granular clay of the eastern archipelago; 9 = granular clay of the central archipelago; 10 = peat of the eastern archipelago; 11 = peat of the Great Barrier; 12 = peat of the eastern reed islands; 13 = peat of the southern border; 14 = peat of the reed islands in the eastern open waters; 15 = blue mud of the central zone; 16 = mud of the northern zone; 17 = mud of the eastern archipelago; 18 = mud of the central open water; 19 = mud of the Great Barrier; 20 = mud of zone A; 21 = mud of zone B; 22 = mud of the southern reed islands; 23 = mud of the eastern archipelago (west of Bol); 24 = mud of the eastern archipelago (east of Bol); 25 = mud of the eastern reed islands.

(Lévêque 1972). Because of their reduced surface some of these biotopes were sampled once, either in 1968 or 1970.

A comparison of mean figures per biotope, using correspondence analysis (Lévêque and Gaborit 1972) enabled us to regroup those communities having fairly similar species composition and to define seven main ecological zones (Tables 5 and 6).

Zone 1 — Archipelago and reed islands of the north (biotopes 6 and 16). conductivity was higher than 500 µS cm^{-1} and molluscs were scarce, consisting mainly of *Melania*.

Zone 2 — Open water of the north and the southern part of the northeastern archipelago (biotopes 9, 15, 17, 18). *Melania* was dominant, but the abundance

Table 5 Mean densities of molluscs by number of individuals m^{-2} in the different biotopes (Fig. 5) sampled in 1968 (after Lévêque 1972).

Zones	1		2				3						4	5	6						7
Biotope No.	6	16	9	15	17	18	3	7	11	13	19	22	5	2	4	8	10	14	23	25	24
Nature of sediment	AG	V	AG	VB	V	V	PS	AG	T	T	V	V	AG	PS	AB	AG	T	T	V	V	V
Number of samples	16	9	1	9	12	22		2	2	8	17	6	24	11	7	5	5	3	14	8	6
Melania	13.3	7.6	314.8	51.5	119.1	160.6	202.8	22.2		14.4	102.3	9.3	197.6	180.4	18.5	0.4	2.6	11.1	1.3	6.3	
Cleopatra	0.9	0.6	75.9	1.2	39.8	4.7	171.8	199.1	37.0	21.8	96.2	12.0	55.0	102.7	64.8	8.1	19.3	130.9	6.1	33.3	1.9
Bellamya	4.6	0.8	174.1	20.4	73.7	21.4	235.7	45.4	5.6	8.3	25.3	1.5	3.9	0.3	0.3	4.5	3.0	1.9	1.9	2.6	
Corbicula					4.0	1.7	166.7	24.1	2.8	10.9	30.6	6.8	9.9	79.4	3.4	10.4	1.1	29.6	1.1	11.3	0.8
Caelatura			7.4		4.0	0.3	11.1	2.8	0.9		1.7	2.5	3.5	1.0	1.6	0.7	1.1		0.5	0.2	
Pisidium	0.6		1.9		1.9		3.2				1.7			6.4			6.4			2.6	
Eupera			3.7		2.3		11.6	37.0	0.9		3.8		0.5	0.5	0.3	0.4		0.9		0.5	
Total	19.4	9.0	577.8	73.1	244.8	168.7	802.9	330.6	47.2	55.4	261.6	32.1	270.4	370.7	88.9	24.5	33.5	174.4	20.9	56.8	2.7

Table 6 Mean density of benthic molluscs by number of individuals m^{-2} in the different biotopes (Fig. 5) sampled in 1970 (after Lévêque 1972).

Zones	1		2				3			4	5	6					7
Biotope No.	6	16	9	15	17	18	11	19	20	5	2	4	10	21	23	25	24
Nature of sediment	AG	V	AG	VB	V	V	T	V	V	AG	PS	AB	T	V	V	V	V
Number of samples	11	7	2	5	30	11	4	9	3	16	27	10	15	4	14	13	20
Melania	1.9	3.5	259.0	185.6	159.3	250.9	34.3	263.9	332.0	94.1	125.9	34.8	4.4	75.6	8.2	10.9	7.2
Cleopatra			28.7	3.0	23.3	9.4	115.7	38.5	103.1	18.1	76.3	63.7	3.9	157.4	11.7	23.1	
Bellamya	0.2		173.1	40.3	41.7	101.9	63.9	6.5	171.7	1.1	0.5	0.9	0.5	4.6	1.7	1.5	0.1
Corbicula					7.0		27.8	22.6	77.2	18.0	73.1	11.1	0.6	29.1	1.5	8.7	0.1
Caelatura			2.8		0.7		6.5	12.6	25.9	2.8	2.2	3.0	0.4	7.4	0.6	0.4	0.1
Pisidium			8.3		0.6		0.9		1.9		1.3					0.1	
Eupera			2.8		0.2	0.4	5.6		3.2		0.4			0.5		0.2	
Total	2.1	3.5	474.7	228.9	232.8	362.6	254.7	344.1	715.0	134.1	279.7	113.5	98.0	274.6	23.7	44.8	7.6

of *Bellamya* in the communities was characteristic of this zone. Molluscs densities were very high.

Zone 3 — 'Great Barrier' and sand banks of the south (biotopes 3, 7, 11, 13, 19, 20, 22). This was a transitional zone between the north and the south basins and the communities were more heterogeneous. *Melania* was still abundant, but *Cleopatra* and *Corbicula* were far better represented than in zone 2, whereas *Bellamya* was scarce. In 1970, *Caelatura* was also seen to be abundant here. Certain biotopes of zone 3 showed some affinities with other zones. In particular biotopes 7 and 11 (granular clay and peat of the Great Barrier) resembled the community of zone 6.

Zone 4 — Open water of the southern basin (biotope 5) *Melania* was dominant, but *Cleopatra* and *Corbicula* were fairly abundant, and *Bellamya* very scarce.

Zone 5 — 'Pseudo-sand' of the southern open water (biotope 2). The 'pseudo-sand' occupied a large area of the southern open water and its community was well defined during 1968 and 1970. *Melania* dominated, but the high abundance of *Corbicula* was especially characteristic of this zone.

Zone 6 — Archipelagos, reed islands and open water of the southeast (biotopes 4, 18, 10, 14, 21, 23, 25). The communities were characterized by the dominance of *Cleopatra*. *Melania* remained well represented, but the rest of the fauna was poor in general, with the occasional exception of *Corbicula*. Density was not very great in most of the biotopes.

Zone 7 — Eastern archipelago (biotope 24). The community was very sparse and identical to that of zone 1 in 1970 (dominance of *Melania*), whereas in 1968 it was very similar to that of zone 6 in structure (dominance of *Cleopatra*).

According to previous observations, it appeared that in 1970 *Melania* was dominant almost everywhere, with the exception of zone 6 where *Cleopatra* dominated. *Bellamya* was well represented particularly in zones 2 and 3, *Corbicula* in zones 3, 4 and 5 and *Caelatura* in zone 3. Zones 1 and 7 were particularly low in molluscs, for which the highest densities were to be found in zones 2 and 3. A fairly clear zonation pattern of mollusc communities was therefore apparent for the whole lake. The geographical situation which may correspond to all the non-identified ecological factors seemed to have considerable importance.

8.3.3 *Insects*

8.3.3.1 *Chironomidae*. Samples taken in 1970, permitted identification of six main ecological zones in Lake Chad, according to which dominant species characterized the community. However, the limits of these zones were not constant throughout the year (Fig. 6).

Zone 1 — with *Cladotanytarsus lewisi* and *Tanytarsus nigrocinctus*. In

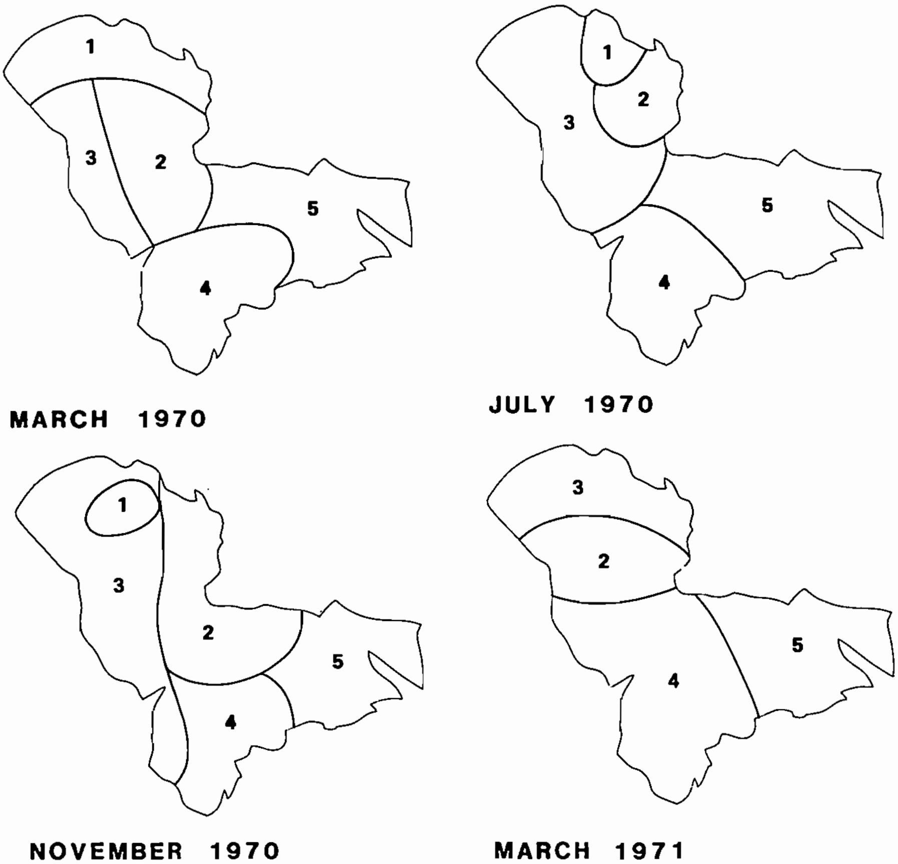

Fig. 6 Zonation of Lake Chad based on the distribution of chironomids (after Dejoux 1976); 1 = zone with *Cladotanytarsus lewisi* and *Tanytarsus nigrocinctus*; 2 = zone with *Polypedilum fuscipenne*; 3 = zone with *Clinotanypus claripennis*; 4 = zone with *Cryptochironomus diceras*; 5 = zone with *Chironomus formosipennis*.

March, this zone covered the north of the lake and these two species, representing 82% of the community were absent from the rest of the lake. In July, *C. lewisi* disappeared, but *Polypedilum fuscipenne* and *Clinotanypus claripennis* were abundant. The presence of *T. nigrocinctus* distinguished this zone, although it was scarce. The zone became more clearly defined in November when *T. nigrocinctus* and *C. lewisi* represented 50% of the community.

Zone 2 — with *P. fuscipenne*. In March 1970 this zone covered the north-eastern archipelago and part of the open water of the north and the Great Barrier. *P. Fuscipenne* was very abundant (60% of total captures) with

Photo 12 Some benthic molluscs.

Photo 13 Boxes used to rear benthic molluscs.

Cryptochironomus stilifer also well represented (14%). In July the zone was reduced to the northeastern archipelago. *Clinotanypus claripennis* (48% of the community) was more abundant than *P. fuscipenne* (23%) and *C. stilifer* had disappeared. In November the zone spread once again to the Great Barrier. *P. fuscipenne* became dominant again (67%) and *C. stilifer* reappeared (27%).

Zone 3 — with *Clinotanypus claripennis*. In March the zone occupied the eastern part of the open water of the north, spreading north and south during the year. *C. claripennis* was abundant and *C. stilifer* was present in notable quantities.

Zone 4 — with *Cryptochironomus diceras* and *Ablabesmyia* sp. This zone, which was the poorest of the whole lake, fluctuated little during the year. *C. diceras* and *Ablabesmyia* sp. were found throughout the year at low densities rarely exceeding 100 individuals m^{-2}.

Zone 5 — with *Chironomus formosipennis*. No species was predominant in this zone which covered the archipelago and the reed islands of the east and southeast. The regular presence of *C. formosipennis* was however, characteristic, together with the three species of *Nilodorum*.

Zone 6 — with *Cricotopus scottae*. This shapeless and patchy zone all over the lake corresponded to the submerged water grasses. It had therefore no precise geographical location. *C. scottae* was largely predominant and *Dicrotendipes fusconotatus* was well represented.

If the changes observed in 1970 are considered characteristic of the seasonal changes affecting the chironomid population, a situation similar to that of March 1970 should have been found in March 1971. But, in fact, certain changes seem to have taken place:

- zone 1 disappeared and *T. nigrocinctus* became scarce;
- zone 2 spread distinctly westwards;
- zone 3 moved northwards, occupying the position of zone 1 in March 1970;
- zone 4 also spread northwards and a species of *Procladius* supplanted *Ablabesmyia* as the characteristic species;
- zone 5 changed little, but *P. fuscipenne*, absent before in this part of the lake, appeared for the first time.

It thus appeared that within one year a community transfer took place, occurring curiously in the same direction as that of the great water masses.

Even over a fairly short time, the chironomid communities appeared to be much less stable than those of worms and molluscs. The rapid development cycles of these insects, together with their great mobility and their great facility for adaptation, were certainly the main causes of the modifications observed in their distribution.

8.3.3.2 *Other insects*. Most species had a very extensive distribution, but the nature of the bottom was an important factor. Thus *Dipseudopsis capensis* and *Eatonica schoutedeni* were found principally on muddy bottoms rich in plant debris, whereas *Ecnomus* sp. and *Cloeon fraudulentum* always lived on clay and sandy bottoms. Generally the density of larvae was greater in the northern basin than in the southern basin of the lake (Carmouze et al. 1972). In the latter, the mean densities were respectively 9, 3 and 21 larvae m^{-2} in March, July and November 1970, whereas they were 36, 26 and 44 larvae m^{-2} in the northern basin. As for the sub-benthic species not living in the sediment, (*Chaoborus anomalus* and *Micronecta scutellaris*), density was also three times lower in the southern basin than in the northern basin.

8.4 Characteristics of the communities

8.4.1 *Distribution of organisms*

A study of the distribution of the molluscs has shown that they have a slight tendency to aggregate (Lévêque 1972). Here we have used Taylor Power law: $S^2 = a\ X^{-b}$. The relationship between the population mean ($\bar{x}$) and the variance (S^2) was obtained for each species from the series of samples from different biotopes and from different stations. The constant (b) was considered an aggregation index characteristic of the species under study. It is equal to 1 if the distribution is uniform and its value exceeds 1 as the individuals of the species studied tend to form aggregates.

In the case of the benthic molluscs of Lake Chad, the mobile prosobranchs ($1.12 < b < 1.84$) had a greater tendency to congregate than the lamellibranchs ($0.92 < b < 1.56$) whose distribution tend to be uniform. In the chironomids (Dejoux 1976), larval distribution was usually aggregated.

8.4.2 *Abundance distribution*

It has been shown that for most communities of benthic molluscs, the number of individuals in each species can be classified according to a geometrical progression law, the law of Motomura (Daget and Lévêque 1969; Lévêque 1972). This law holds (Inagaki 1967) when the correlation coefficient, calculated between the numbers and rank of each species (classified in decreasing order of numbers) is higher than 0.95. When it is not confirmed ($r < 0.95$), it may be concluded that the community was going through a period of change or else that the sampling was inadequate.

One interesting aspect of this law is that it permits the definition of 'nomocenoses' (Daget et al. 1972). They can be characterized by three parameters: the number of species; the environmental or Motumura (m), constant which is the linear regression slope between the numbers and ranks and which corresponds to a diversity index; the density of the community.

These parameters have been calculated for the communities of the Bol region and for the whole lake sampled in 1970 (Table 7). The law of Motomura proved true in most cases signifying that fairly stable communities existed and were well sampled.

8.4.3 *Characteristic species of biotopes*

These species may be investigated by the minimal deviation method (Bonnet 1964). We applied it to communities sampled at Bol in 1970 (Dejoux et al. 1971; Lévêque 1972; Dejoux 1976). Among the oligochaetes, *Naïs* and *Aulophorus* which were well represented in the periphyton, were always found on sandy bottoms near submerged vegetation as in the case of the zone under study. *Alluroides* and *Pristina* were abundant on clay beds and *Aulodrilus* in the mud and sand. Among the molluscs, *Melania* was typical of mud bottoms, *Bellamya* of granular clay; *Corbicula* and *Caelatura* of clays. There were no characteristic species of peat or sand. In comparison with the two preceding groups, the insects had relatively few characteristic species for any type of bottom. However, *E. dispar* and *C. fraudulentum* were found in granular clay and *N. rugosum* and *Chrionomus* sp. 7 in soft clay, *C. claripennis* in mud, *A. dusoleili, Stictochironomus* sp. 2 and *Tanytarsus* sp. 1 in peat, *C. lewisi, Cryptochironomus* sp. 1 and sp. 2 and *Polypedilum* sp. 3 in the sand.

The characteristic species of a bottom type did not necessarily constitute a biological association and were only valid for the zone studied at a given time, i.e. in well-defined ecological conditions. Thus, even though characteristic mollusc species were found in the biotopes sampled in 1970 over the whole lake (Lévêque 1972), the same results were not necessarily found at Bol at the same time. *Melania* was not characteristic of any biotope whereas *Corbicula* was characteristic of the blue clay sand and pseudo-sand beds and *Caelatura* of sand and mud bottoms of the Great Barrier. Many biotopes, had no particular typical species. This was also true of the insects, although *C. lewisi* was characteristic of sand over the whole lake and at Bol. Other species were found in the mud and granular clay, while peat and soft clay had no characteristic species (Dejoux 1976).

8.4.4 *Interspecific relations*

The study of affinities between species was based on the assumption that species from different samples whose numbers varied in a similar manner all had common ecological requirements. These affinities have been examined in mollusc samples taken at Bol in 1967 and 1970 and over the lake in 1970 (Fig. 7). With the exception of a strong affinity between *Corbiculá* and

Table 7 Abundance distributions of benthic molluscs in different biotopes of the Bol Region and Lake Chad in 1970 (cf. Fig. 5 for the biotope numbers). Values of the parameters defining the nomocenoses: density, Motomura constant (m) and number of species; r = the correlation coefficient between the ranks and the abundance of species (after Lévêque 1972).

Biotopes	A at Bol	G at Bol	T at Bol	S at Bol	V at Bol	1	2	4	5	9	10	11	17	18	19	20	21	23	25
Sampled surface in m^2	8	8	13	7	19	5.5	13.5	5	8	1	7.5	2	15	5.5	4.5	1.5	2	7	6.5
Density m^{-2}	61.6	277	34.8	23	25	258.4	301.8	122.2	144.9	513	30.7	275	251.5	391.6	371.3	772	296.5	25.1	48.5
r	0.952	0.968	0.921	0.898	0.988	0.970	0.948	0.993	0.975	0.973	0.932	0.970	0.990	0.971	0.957	0.963	0.980	0.969	0.981
m	0.417	0.414	0.374	0.488	0.290	0.381	0.325	0.335	0.336	0.354	0.353	0.472	0.313	0.108	0.424	0.410	0.329	0.454	0.347
Number of species	7	6	6	5	5	7	7	5	5	6	5	7	7	4	5	7	6	5	6

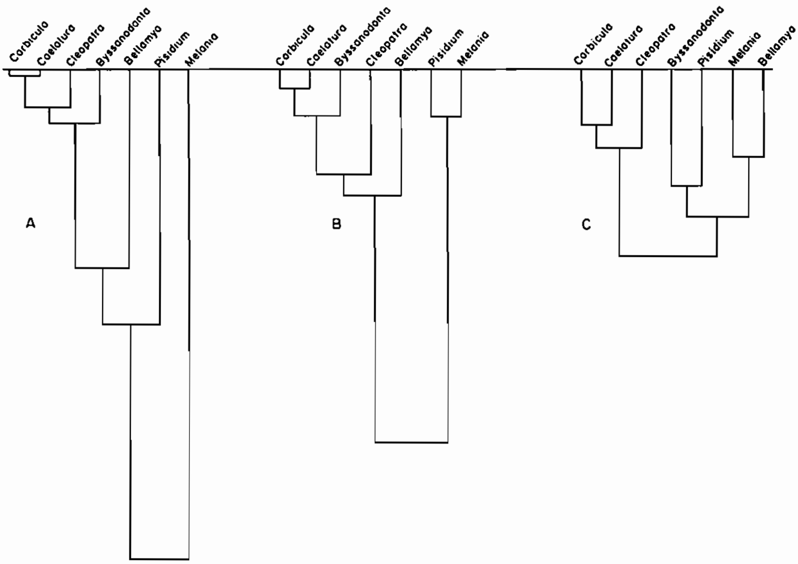

Fig. 7 Interpretation of the interspecific correlation matrices by the dendrogram method for molluscs; A = Bol, 1970; B = Bol 1967; C = whole lake, 1970.

Caelatura found in three series of observations, the other results did not agree. It may be considered then that relations revealed in a given situation are mere coincidences that must be verified elsewhere at other times to ensure their validity.

8.5 The benthic biomass

8.5.1 *Mean weight of the principal species and conversion factors*

The mean alcohol weight of the worms was evaluated as 3.41 mg for Alluroïdidae, 0.35 mg for Tubificidae and 0.06 mg for Nematodes. The dry weight was estimated at around 12% of the alcohol weight and the energy content at 5300 cal g^{-1} of the dry weight (Cumins and Wuycheck 1971).

For the principal species of benthic molluscs, the mean alcohol weight, the dry body weight, and the weight of the shell have been calculated (Table 8) from samples taken in 1970 over the whole lake. The energy content was 4000 cal g^{-1} for the different species (Lévêque 1973) (body without shell).

Finally, for the insects (Table 9), the fresh and dry weight of some species were determined by different methods (Dejoux 1976). The energy content was estimated as an average of 5300 cal g^{-1} dry weight, similar to the oligochaetes.

Table 8 Mean alcohol weight (in mg), dry body weight and shell weight for the main benthic species of Lake Chad collected in 1970.

	Alcohol weight (A.W.)	Dry body weight (D.B.W.)	A.W./D.B.W. (%)	Shell weight (S.W.)	S.W./A.W. (%)
Melania	88	6.6	7.5	48	55
Cleopatra	178	30.3	17	107	60
Bellamya	652	52.2	8	300	46
Corbicula	232	6.3	2.7	153	66
Caelatura	1571	78.6	5	1037	66

8.5.2 *Distribution of benthic biomass in Lake Chad*

8.5.2.1 *Worms.* The biomass distribution in March, July and November 1970 is shown in Fig. 8. It will be noted that the highest values were found in March and the lowest in July, corresponding to the seasonal abundance cycle observed in this group of invertebrates. Nevertheless, the biomass on the pseudo-sand and clay sediments of the southern open water, composed almost exclusively of Alluroïdidae, remained relatively important throughout the year. Variations were more marked in other zones where the Tubificids were dominant.

8.5.2.2 *Molluscs.* The number of individuals and the biomass have been calculated for the different species for each biotope sampled in 1970, using, the mean numbers per biotope (Tables 5 and 6), the surface occupied, and the mean individual weight. In order to obtain an estimate for the whole lake, the results obtained in 1968 from the biotopes 3, 7, 13 and 22, which were not sampled in 1970, were also considered.

The total number of benthic molluscs was 3.5×10^{12} individuals in 1970, made up of 61% *Melania*, 15% *Cleopatra*, 15% *Bellamya*, 8% Corbicula, and 1% *Caelatura*. A comparable value of 3×10^{12} individuals was obtained in 1968 (Lévêque 1972).

Expressed as dry body weight, the molluscs biomass totalled 64 000 tons in Lake Chad in 1970, for a water surface area estimated at 19 200 km^2. In terms of proportion of the biomass, 93% of the total consisted of three species: *Bellamya* (43%), *Cleopatra* (23%) and *Melania* (22%). the Lamellibranchs *Caelatura* (5%) and *Corbicula* (2%) were less common. The biomass of shells was 410 000 tons.

The biomass was not uniformly distributed in the lake (Fig. 9), since mean values between 0.2 and 200 kg ha^{-1} were observed, varying with biotopes. The highest values recorded, between 35 and 200 kg ha^{-1}, occurred in the open

Table 9 Mean wet and dry weight of larval insect species of Lake Chad.

Species	Fresh weight (mg)	Dry weight (mg)
Chironomidae		
Chironomus formosipennis	3.08	
Cryptochironomus stilifer	0.56	0.03
Cryptochironomus diceras	2.41	
Polypedilum fuscipenne	2.35	0.33
Tanytarsus nigrocinctus	0.45	
Cladotanytarsus lewisi	0.27	
Cladotanytarsus pseudomancus	0.25	
Rheotanytarsus ceratophylii	0.40	
Dicrotendipes fusconotatus	0.78	
Cricotopus scottae	0.84	
Ablabesmyia dusoleili	0.35	
Procladius brevipetiolatus	1.42	
Clinotanypus claripennis	2.50	0.39
Nilodorum rugosum	7.45	0.75
Chaoborus anomalus	1.89	0.04
Ceratopognus sp.	0.43	0.026
Ephemeroptera		
Eatonica schoutedeni		3.0
Cloeon fraudulentum		0.04
Povilla adusta		1.0
Trichoptera		
Ecnomus dispar		1.5
Dipseudopsis capensis		2.5
Hemiptera		
Micronecta scutellaris		0.07

water and archipelago of the north basin, and around the Great Barrier. In the extreme north and east of the lake much lower values were obtained.

8.5.2.3 *Chironomidae*. As with oligochaetes, a seasonal abundance cycle was observed for this group, with minimal biomass in July (Fig. 10). The northern basin was richer than the southern basin. This phenomenon could be related to the greater ecological stability of the slightly deeper northern basin, which was not directly affected by the flood waters of the Shari, as was so in the southern basin.

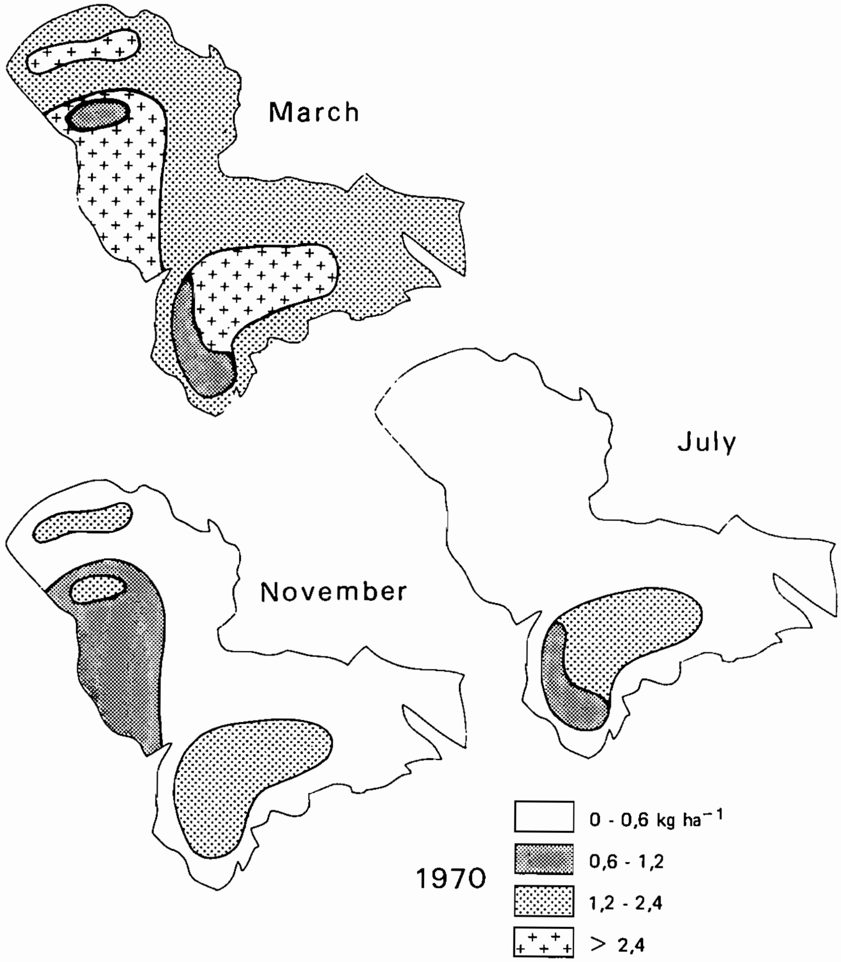

Fig. 8 Distribution of benthic oligochaete biomass (dry weight) in March, July and November, 1970, over the whole lake.

It should be noted that this group of invertebrates had a fairly rapid biological cycle and great facility of movement, in contrast to those mentioned earlier, and this probably accounted for the greater variations observed between two sampling periods.

8.5.3 *Estimation of benthic invertebrate biomass in 1970*

The zonation patterns proposed for the three groups of benthic invertebrates did not overlap exactly, because the distribution factors did not all have the

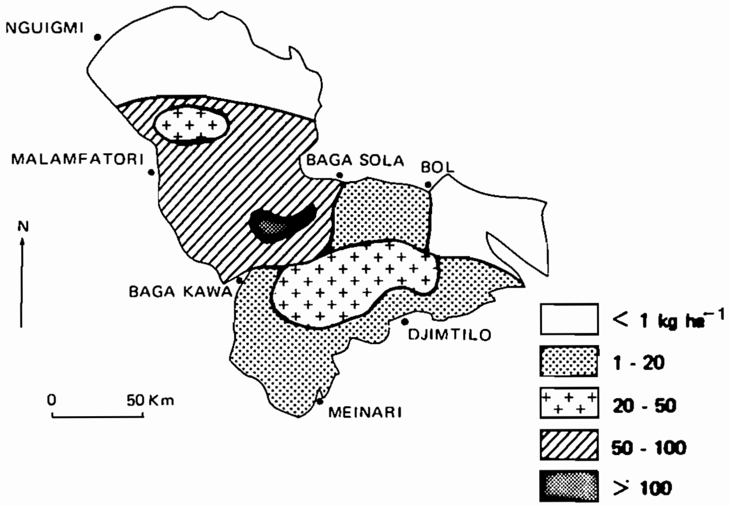

Fig. 9 Distribution of benthic mollusc biomass (dry weight, shell free) in March, 1970, over the whole lake.

same significance for each. It should be emphasized that a distinct difference seemed to exist between the north and south basins for all groups, as well as between the open water zone and the archipelago. On the basis of the distribution of the molluscs, which consitituted the bulk of the biomass, seven zones could be clearly defined (Fig. 11). For each, the mean biomass (dry weight) of the three groups studied in March 1970 (Table 10) has been calculated. For the whole lake, the mean biomass of molluscs (33 kg ha^{-1} d.w.) was about 11 times greater than that of the worms (2.9 kg ha^{-1}) and 27 times greater than that of the insects (1.2 kg ha^{-1}). The mean biomass of shells was approximately 210 kg ha^{-1}. The total bentic biomass was estimated to be 71 100 tons composed of 5500 tons of worms, 2300 tons of insects and 63 000 tons of molluscs. Most of the biomass (74%) was concentrated in zones 2, 3 and 4, corresponding to the open water of the north, the northeastern archipelago and the Great Barrier, which represented no more than 40% of the lake surface. The energy value of the total benthic stock was 294 540 × 10^{6} Kcal, of which 29 200 × 10^{6} Kcal was contributed by the worms, 12 190 × 10^{6} Kcal by the insects and 253 000 × 10^{6} Kcal by the molluscs. The average energy value was 152.4 × 10^{3} Kcal ha^{-1}. The above estimations only concerned the benthos and completely excluded the invertebrate communities associated with the aquatic macrophytes. This was a major omission in so far as aquatic vegetation stands in Lake Chad were estimated to cover about 2000 km^{2} in 1970 (clumps of *Potamogeton* or *Ceratophyllum, Papyrus, Phragmites* or *Typha*). Such habitats were some-

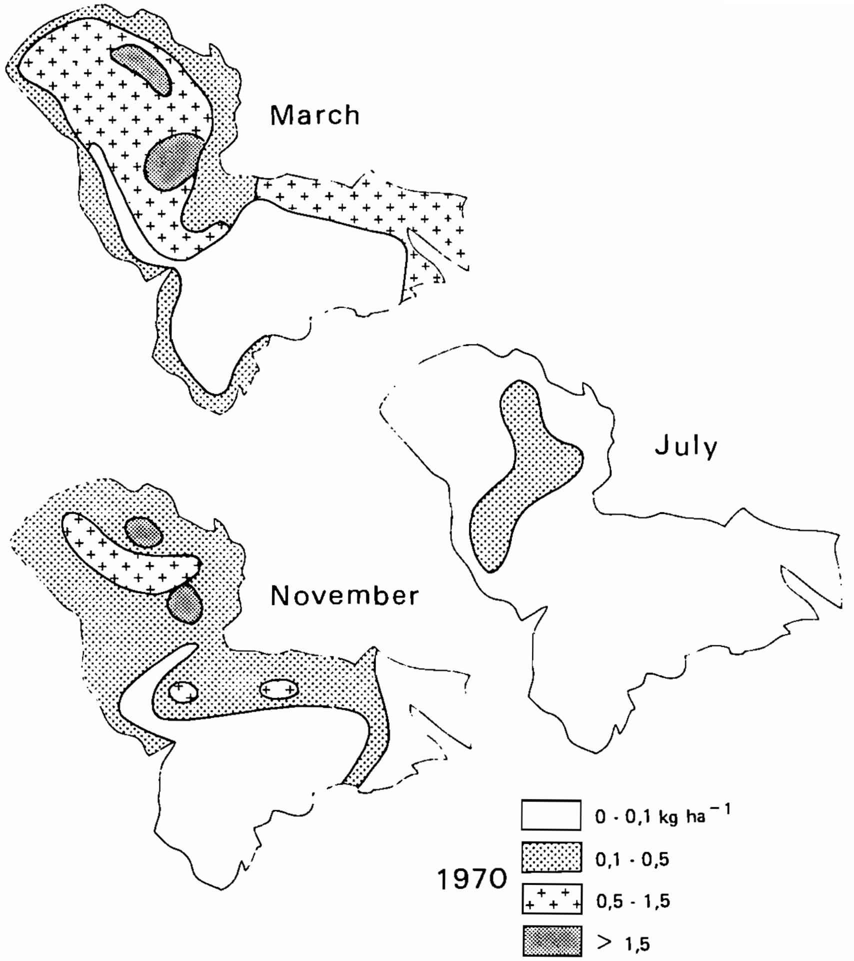

Fig. 10 Chironomids: distribution of biomass (dry weight) in March, July and November, 1970, over the whole lake.

times fairly rich in insects, pulmonate molluscs and worms (Naididae in particular).

8.6 Temporal community changes

Throughout the period during which the benthic communities were studied, the level of Lake Chad never ceased to drop. This phenomenon, fairly discreet until 1970, accelerated later until in 1973 the north and south basins separated. Later the north basin dried up (1975).

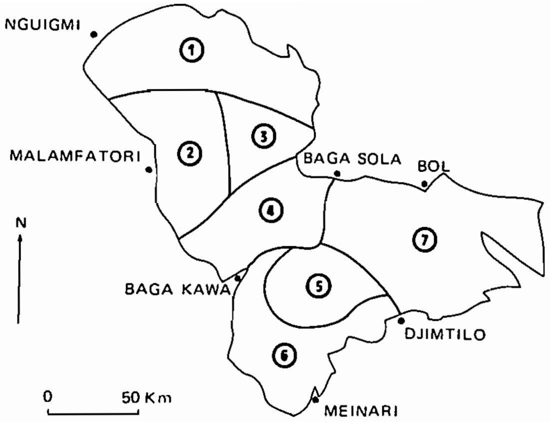

Fig. 11 Zonation pattern of the benthic fauna in Lake Chad in 1970 (cf. Table 10) (after Carmouze et al. 1972).

Unfortunately it was impossible to simultaneously study the changes within the benthic communities for all groups in the whole lake. We do however have some information showing that significant changes occurred in certain zones.

8.6.1 *Molluscs*

The temporal changes of the malacological communities had been observed in the four bottom types of the southeastern archipelago (Bol region) where sampling was carried out in January 1967, 1970 and 1972 (Carmouze et al. 1972). The density of all species in all biotopes diminished generally from 1967 to 1972 (Table 11), with the exception of *Cleopatra* and *Melania* which, in 1970, became abundant in granular clay substrata and in mud substrata respectively. Regular sampling from 1967 to 1970 made it possible to follow more precisely the changes occurring in the mollusc communities on clay and mud bottoms. The most important changes occurred in 1968 and included a rapid decrease in the density of *Cleopatra* in the mud, followed by a slow increase in *Melania*, and finally the dominance of this species in 1970. At the same time *Bellamya* and *Eupera* decreased in granular clay and *Eupera* declined in soft clay (Fig. 12).

The temporal changes revealed in the southeastern archipelago were also observed in other regions of the lake. The mean numbers of species in the biotopes investigated during 1968 and 1970 (Fig. 13) were compared by factorial analysis (Lévêque and Gaborit 1972). This shows that the position of some biotopes, tended to move towards the left and the base of the graph in relation to axes 1 and 2, between 1968 and 1970. This observation may be explained by the fact that the relative density of *Melania*, in comparison with

Table 10 Mean benthic invertebrate standing stocks during 1970 in the seven main ecological zones of Lake Chad (Fig. 11).

Zones	Surface (km²)	Mean biomass in dry weight (kg ha⁻¹)				Mean biomass in kcal ha⁻¹ × 103
		Worms	Insects	Mollusca	Total	
1	3082	2.1	1.4	0.2	3.7	19.4
2	3871	8.0	2.1	64.2	74.3	310.3
3	1501	1.1	2.9	47.8	51.8	212.4
4	2133	1.9	1.6	72.0	75.5	306.5
5	2290	1.5	0.1	38.6	40.2	162.9
6	2083	2.6	0.1	11.8	14.5	61.5
7	4259	0.8	0.6	10.6	12.0	49.8
Mean for the whole lake		2.9	1.2	33.0	37.1	153.0

that of *Cleopatra*, increased in the biotopes examined in 1970, just as that of *Corbicula* increased more than that of *Bellamya*. The most spectacular example was that of biotope 24 (mud of the southeastern archipelago west of Bol and peat of the Great Barrier).

Only a few fragmentary results were obtained in 1972 in two biotopes of the open water of the east (Table 12). The pseudo-sand community had changed little during the preceding four years, either in structure or the species density. In the blue clay (the biotope neighbouring the southeastern archipelago), however, densities which had been fairly comparable in 1968 and 1970, had decreased considerably by 1972, thus coinciding with observations from the Bol region.

It is difficult to accurately determine the factors which provoked the observed changes in the malacological communities between 1967 and 1972, but, either directly or indirectly, the lower level of the lake was certainly largely responsible for these modifications. The shallower the lake, the greater the effect of waves on bottom sediments. With loose beds, the surface sediment may become partly suspended greatly perturbing ecological conditions, since the environment becomes highly unstable. A layer of very fluid mud may even develop at the water–sediment interface, reducing the mollusc survival which have a tendency to sink into the mud because of their weight. Furthermore, the waters become loaded with silt, as noticed in the Bol region (Lemoalle 1974) and this can be harmful to the small lamellibranch filter-feeders. On bottoms such as pseudo-sand (Table 12), where larger and heavier particles predominated, this phenomenon must have been less evident. Thus the communities of this substratum altered little between 1968 and 1972.

Table 11 Changes in the mean density of benthic molluscs, as number of individuals m^{-2} in the Bol region (southeastern archipelago) in January 1967, 1970 and 1972 (after Carmouze et al. 1972).

Species	Sediment type											
	Soft clay			Granular clay			Mud			Peat		
	1967	1970	1972	1967	1970	1972	1967	1970	1972	1967	1970	1972
M. tuberculata	2.0	0.3	0	1.0	1.1	0.4	0.6	18.5	1.8	4.8	6.6	3.3
C. bulimoides	121.7	48.1	0	37.2	222.4	1.5	7.2	3.2	0	37.6	24.9	5.9
B. unicolor	3.1	0.7	0	14.8	2.5	0.6	0.6	0.6	0.2	5.1	0.2	0.4
C. africana	66.3	5.4	0.4	62.4	15.4	1.7	0.5	0.8	0.2	0.3	0.4	3.3
C. aegyptiaca	11.0	1.6	0.2	4.0	3.1	3.2	0	0.1	0.4	0.2	0.1	0.2
P. pirothi	5.7	0.1	0	3.0	0	0	0	0	0	3.5	0.1	0.6
E. parasitica	16.8	0.1	0	97.2	11.1	0	0.2	0	0	0	0	0
Total	226.6	56.3	0.6	219.6	255.6	7.4	9.1	23.2	2.6	51.5	32.3	13.7

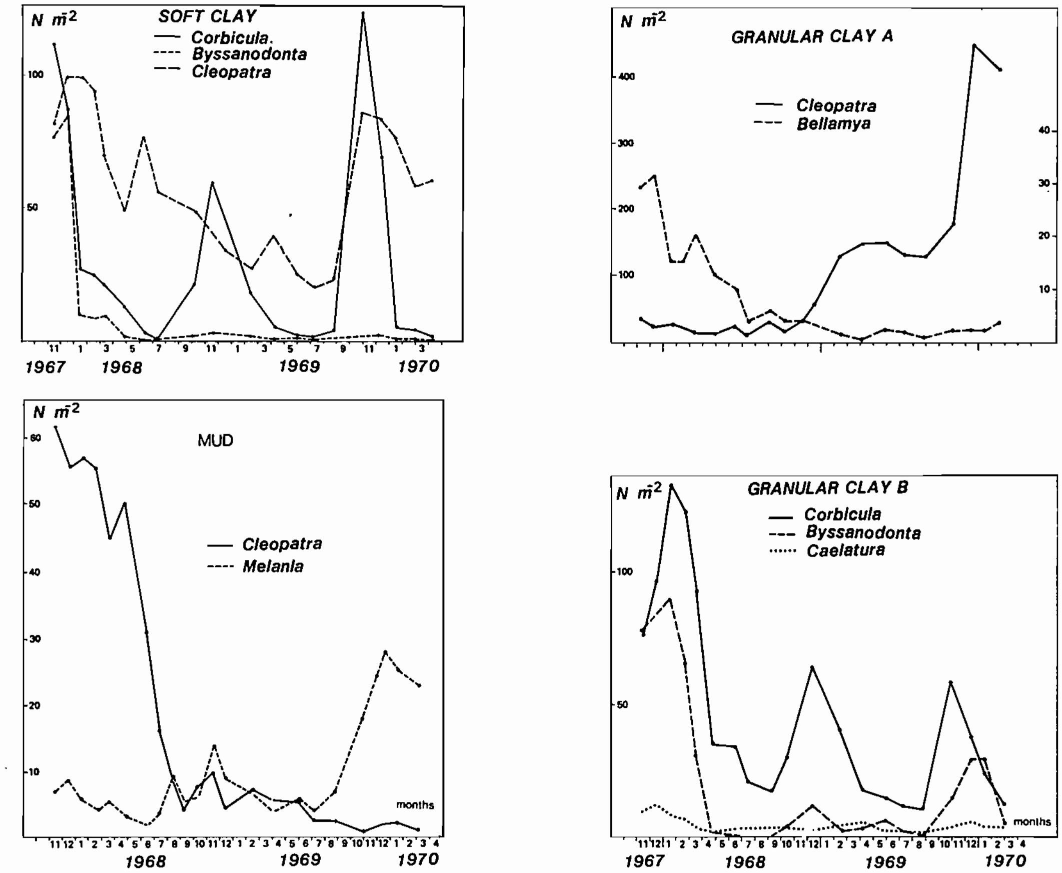

Fig. 12 Variations in the density of the main mollusc species on three bottom types in the Bol region (eastern archipelago), in November 1967, and March 1970 (after Lévêque 1973).

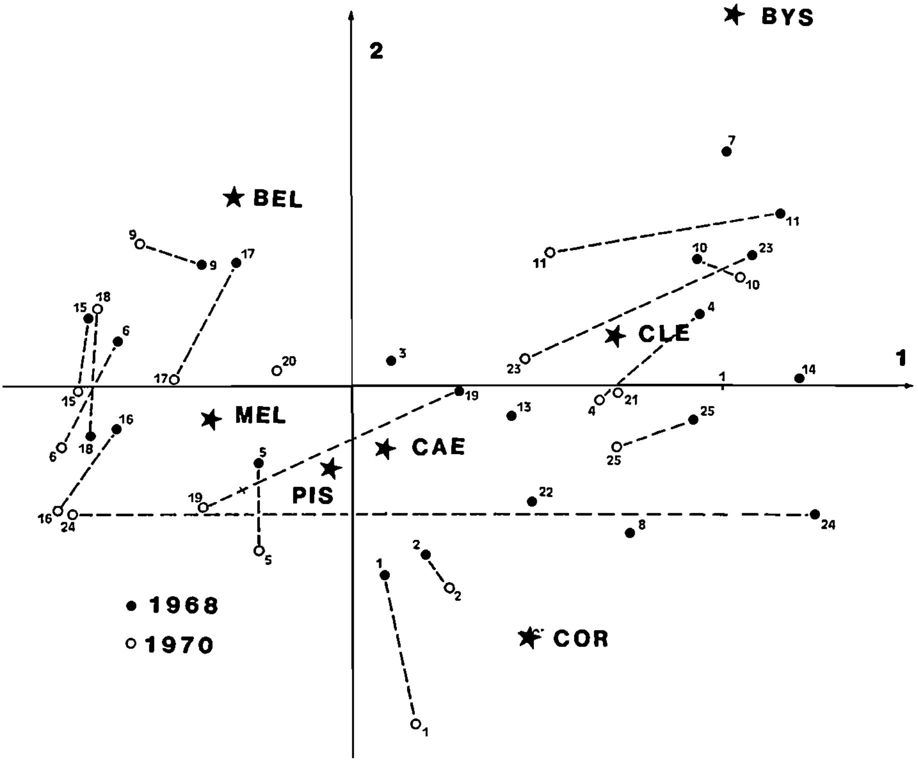

Fig. 13 Position on axes 1 and 2 of the mollusc species and mean plot readings in the biotopes sampled during 1968 and 1970 in Lake Chad (after Lévêque and Gaborit 1972).

8.6.2 *Chironomids*

We have already seen that the aquatic insect communities were fairly unstable over the course of a year. The same was true between years as shown by samples taken with a light trap between 1965 and 1974 at various points of the lake (Dejoux 1976).

In the southeastern archipelago (Bol region) a change in the dominant species was observed and particularly important was a decrease in the number of species collected between 1965 to 1974 (Table 13). On the other hand, species that were abundant and typical in the north of the lake in 1970 (*C. stilifer* and *T. nigrocinctus*) became dominant in 1972 and 1974 at Bol.

In the Shari delta (Table 14) the same phenomena were observed, but the decrease in the number of species was less spectacular than at Bol. In fact, at this station, lake species mingled with river species and the latter seemed to have been less affected than the others by the fall in lake level. This was for example

Table 12 Changes in mean density of the major species of benthic molluscs as number of individuals m^{-2} on the pseudo-sand and blue clay substrata of the southeastern open water in 1968, 1970 and 1972 (after Carmouze et al. 1972).

Species	Biotope 2			Biotope 4		
	pseudo-sand			blue clay		
	1968	1970	1972	1968	1970	1972
M. tuberculata	181	126	139	19	35	1
C. bulimoides	103	76	78	65	64	11
B. unicolor	1	1	0	0	1	0
C. africana	80	73	54	4	11	1
C. aegyptiaca	1	2	1	2	3	1
Total	366	278	272	90	114	14

the case, with *P. longicrus* and *P. griseoguttatum* which were collected fairly regularly. Among the lacustrine species, such as *P. maculosus* and *C. melutensis*, the same phenomenon occurred as at Bol, with sudden appearance or disappearance. At the same time *T. nigrocinctus* was also abundant in 1974.

8.7 Conclusions. Comparison with other lakes of the intertropical zone

Due to its shallow depth, Lake Chad, as a whole, can be considered as a vast littoral zone where the benthic communities are subjected to the combined action of several ecological features. One of the most important is the annual fluctuation of the water level under the influence of the Shari flood waters together with between year fluctuations dependent upon hydrological budget and the climatic 'past' of the system. During the period of our observations, a progressive fall in the level of the lake was evident, accompanied by modifications in the structure and density of the benthic populations. Thus, between 1967 and 1972, the malacological communities changed progressively and their densities decreased considerably on loose substrata. As the level of Lake Chad has fluctuated considerably since the beginning of the century, the majority of the benthic communities have probably been constantly disturbed, occasionally reaching extreme situations when they disappear completely (e.g. the north basin dried up in 1975). An identical phenomenon has recently occurred in another shallow African lake: Lake Chilwa.

During the period under study, which corresponded to the 'Normal Chad'

Table 13 Changes in the composition of the chironomid communities of the Bol region from 1965 to 1974, based on catches by light trap (Dejoux 1976).

Species collected (%)	1965	1966	1971	1972	1974
Polypedilum deletum	34	0.1	0	0	0
Polypedilum abyssiniae	42.1	0.5	0	0	0
Procladius brevipetiolatus	0	62.4	1.6	0	0.05
Polypedilum longicrus	3.4	6.8	15.5	0	0
Ablasbesmyia dusoleili	0.1	0.2	36.1	0	0.05
Cryptochironomus stilifer	0	0	34.9	88.1	0
Cladotanytarsus pseudomancus	0.3	0	0	0	14.3
Tanytarsus nigrocinctus	0.2	2.7	0	0.03	80.7
Total number of individuals collected in the year	69 143	4530	180	3399	5420
number of species collected	58	30	8	6	12
Equitability (%)	40.4	43.2	69.6	23.1	26.4

period, the mean biomass for the whole lake was approximately 3.7 g m^{-2} (dry weight). It will be recalled however, that vast zones of aquatic vegetation mats existed in Lake Chad, where insects were abundant. Nevertheless, the dominance of molluscs in the benthic biomass should be stressed, for it is a fairly infrequent phenomenon. Most of the stock was concentrated in the north basin and the Great Barrier. No definitive explanation was found for the relative paucity of this group in the south basin but it was probably related to the greater hydrological instability of this area. As the north basin was a little deeper than the south basin and did not receive the direct inflow of the Shari water, it could be considered as being truly lacustrine, whereas the south basin was merely an extension of the river system, influenced by disturbances from floods (Carmouze et al. 1972). It was also possible that the distribution of biomass was influenced by predation, which was not necessarily of the same intensity in different regions of the lake and on different species. The lack of quantitative data in this field, however, makes it impossible, at present, to estimate its importance.

The benthic communities and biomasses of tropical African lakes have been the subject of few quantitative research studies. Therefore it is worthwhile to examine the information at our disposal and to compare it with the results obtained in Lake Chad.

Table 14 Changes in the dominant species of the chironomid communities in the Shari delta from 1965 to 1974, based on catches by light trap (Dejoux 1976).

Species collected (%)	1965	1966	1968	1971	1972	1973	1974
Polypedilum abyssiniae	12.6	1.2	0	0	0	17.3	1.3
Ablabesmyia pictipes	18.0	6.6	0	0	0	0.5	0
Polypedilum griseoguttatum	23.3	2.7	23.3	0	0	2.4	8.6
Cryptochironomus dewulfianus	0.3	28.5	0	0	1.2	0.4	2.1
Polypedilum longicrus	3.4	52.6	0	40.2	0.7	9.6	22.6
Procladius maculosus	0	0	19.5	0	0	0	0
Clinotanypus claripennis	1.5	0.6	19.5	0	0	0	0
Ablabesmyia dusoleili	1.2	1.3	15.6	2.4	0.3	3.2	0.4
Cryptochironomus melutensis	0	0	0	0	73.1	0	0
Cryptochironomus nudiforceps	0.1	0	0	8.5	0.4	22.1	0.05
Cladotanytarsus pseudomancus	0.4	0	0	0	9.2	29.6	25.0
Tanytarsus nigrocinctus	0.3	0	0	0	0.2	3.1	34.5
Total number of individuals collected in the year	4914	834	71	82	1326	4718	6720
Number of species collected	49	20	11	18	14	23	18
Index of diversity	3.602	1.991	2.701	3.090	1.470	2.044	2.834
Equitability (%)	64.2	46.1	78.1	74.1	38.6	52.1	66.7

In Lake Léré (Chad), the mean biomass was estimated at 2.6 $\mathrm{g\,m^{-2}}$ (dry weight) for February 1970 (Dejoux et al. 1971). This value is comparable to that of Lake Chad. Further, the molluscs also dominated this system (2 $\mathrm{g\ m^{-2}}$, shell-free dry weight).

A series of lakes in the region of the White Nile has been studied by Monakov (1969). The benthic standing crop varied between 0.1 and 0.5 $\mathrm{g\ m^{-2}}$ (estimation in dry weight). Oligochaetes were dominant but molluscs were sometimes well represented.

Lake George is a shallow lake which has a mean depth of 2.4 m. In this system, the ecological factors vary little with the seasons, due to its situation below the equator (Burgis et al. 1973). The superficial sediment consists essentially of very soft mud, rich in organic matter, and the first 6 to 10 cm of this are often resuspended by the action of the wind (Viner and Smith 1973). The benthic fauna (Darlington 1977) is composed mostly of Dipteran larvae (*Chaoborus*, chinoromids). Close to the shore, it is more diversified and the gastropod *Melanoides tuberculata* is found. The absence of this species from most of the central regions of lake may be explained by the presence of unstable and the excessively fluid superficial sediments. The mean standing crop was approximately 1.2 g m^{-2} (dry weight) (Burgis et al. 1973).

Like Lake Chad, Lake Chilwa (Malawi) is a shallow endorheic lake with a level susceptible to considerable annual variations (McLachlan and McLachlan 1969; MacLachlan 1979). Observations on the benthic fauna were made in 1967, during a period of severe drought. At this time the fauna was very sparse and comprised only a few species of chironomids, Coleoptera and Hemiptera. However a study of the remains and debris of the fauna, thought to represent the benthic communities existing just before the fall in Lake level, showed that the number of species was originally far greater and that there were many molluscs. Among these, benthic species identical to those of Lake Chad (*Bellamya unicolor, Melanoides tuberculata*), as well as *Lanistes, Aspatharia* and diverse pulmonates were found. The benthic biomass, estimated in 1967 at 0.07 g $m–^{2}$ (dry weight) in one region of the lake, must therefore have been considerably higher before the level fell and it may be supposed that molluscs constituted a large part of it, as in the case of Lake Chad. The disappearance of numerous benthic species could perhaps be due to an increased salinity of the water caused by the evaporation accompanying the drought. When the lake was flooded again in 1969, the mud substrata were rapidly colonized by *Chironomus transvaalensis*, but this species had practically disappeared ten weeks later (Maclachlan 1974). The benthic fauna, in 1969 and 1970, consisted mainly of insect larvae; the molluscs, apparently, not yet having had time to recolonize the sediments.

In Lake Turkana (ex-Rudolph), which reaches 80 m in depth, some observations have been made by Ferguson (1975). The benthic fauna was poor but was generally more abundant in the littoral zone than in deeper areas. Below 10 m, the community consisted mainly of two mollusc species (*Cleopatra pirothi* and *Malanoides tuberculata*), four species of chironomids and five species of ostracods. The abundance of these species diminished down to 80 m, where only *C. pirothi* and one chironomid species were found. The Ostracoda disappeared at 20 m. Oligochaetes were scarce beyond the littoral zone. Ferguson (1975) gives no estimation of the biomass. No explanation has been found so far for the scarcity of benthic fauna in Lake Turkana. It seems to have no connection, as in other lakes, with the oxygen content of the bottom water, which rarely decreases below 70% saturation at 80 m. It should be noted that the high conductivity of the Lake Turkana water (around 3000 μS cm^{-1}) did not appear to hinder the presence of molluscs, as in Lake Chad. One species (*M. tuberculata*) was found in both systems, and we must presume that the water composition differs or that the limit of conductivity observed in the north of Lake Chad is a mere coincidence and results from the intervention of other non-identified factors.

The benthic biomass of Lake McIlwaine (Rhodesia), a reservoir with a mean depth of 10 m (31 m maximum), can be estimated at about 3 g m^{-2} (dry weight), from Munro's data (1966). Insects and oligochaetes were dominant in 1962–1963. Later observations in 1968 (Falconer and Marshall 1970) showed that the 2–4 m deep zone was the richest and that below 5 m, no animals were found, probably due to the absence of oxygen at the bottom together with the high ammonia content. Moreover, Lamellibranchs were seen to disappear (especially *Sphaerium*) in 1968–1969. This was probably due to a very sharp drop in lake level during 1967–1968, which caused a large part of the littoral zone to dry up. Chironomid larvae were still dominant in the benthic fauna during 1968–1969, but less abundant than in 1962–1963 (similar to the oligochaetes).

The research by Petr (1972) in Lake Volta, during the years following the closing of Akosombo dam, deals essentially with the establishment of benthic communities. With the exception of *Pisidium*, molluscs were chiefly represented by the pulmonates, the abundance of which was linked to the presence of aquatic plants, as in Lake Chad (Lévêque 1975). The same was true for the oligochaetes, which were represented by the Naididae. Chironomids were largely dominant throughout the lake, at least during the first years of its filling and the Ephemeroptera, *Povilla adusta* was also an extremely important component of the benthic community during this filling phase in the development of the lake.

In Lake Kariba, a reservoir created in 1958, McLachlan and MacLachlan (1971) showed that chironomids largely dominated the benthos. Molluscs (represented by a pulmonate species) and oligochaetes were scarce. The total biomass was low, between 0.02 and 0.1 g m^{-2} (dry weight). However standing stocks recorded ponds along the shoreline were higher (1.4 g m^{-2}).

In comparison, the biomasses observed in certain lakes of Central Amazonia (Filtkau et al. 1975) are generally much lower (0.02 to 0.9 g m^{-2} and insects usually dominate.

It is impossible here to give an exhaustive account of the results obtained in other lakes around the world. It should be mentioned, however that Cole and Underhill (1965) give values for benthic biomass ranging between 4.3 and 8.6 g m^{-2} for seven lakes in North America, which they considered to be the most productive. The values are higher than the mean values observed in Lake Chad in 1970, but comparable to those of the north basin and the Great Barrier (Table 10). In Lake Esrom (Denmark), the mean biomass of 16.5 g m^{-2} is one of the highest ever observed (Jonasson 1972), but on the whole the benthic biomass of European lakes ranges from 0.2 to 2 g m^{-2}. We may therefore consider Lake Chad, and in particular the northern basin, to be one of the richest lakes as regards benthic biomass. Higher biomass values are generally found for invertebrates inhabiting aquatic vegetation mats. No data are available for Lake Chad, but in the south temperate coastal lake Smartvlei, Davies (personal communication) observed mean standing stocks of 132 g dry weight m^{-2} (summer) and 34 g (winter), the mussel *Musculus virgiliae* being dominant too.

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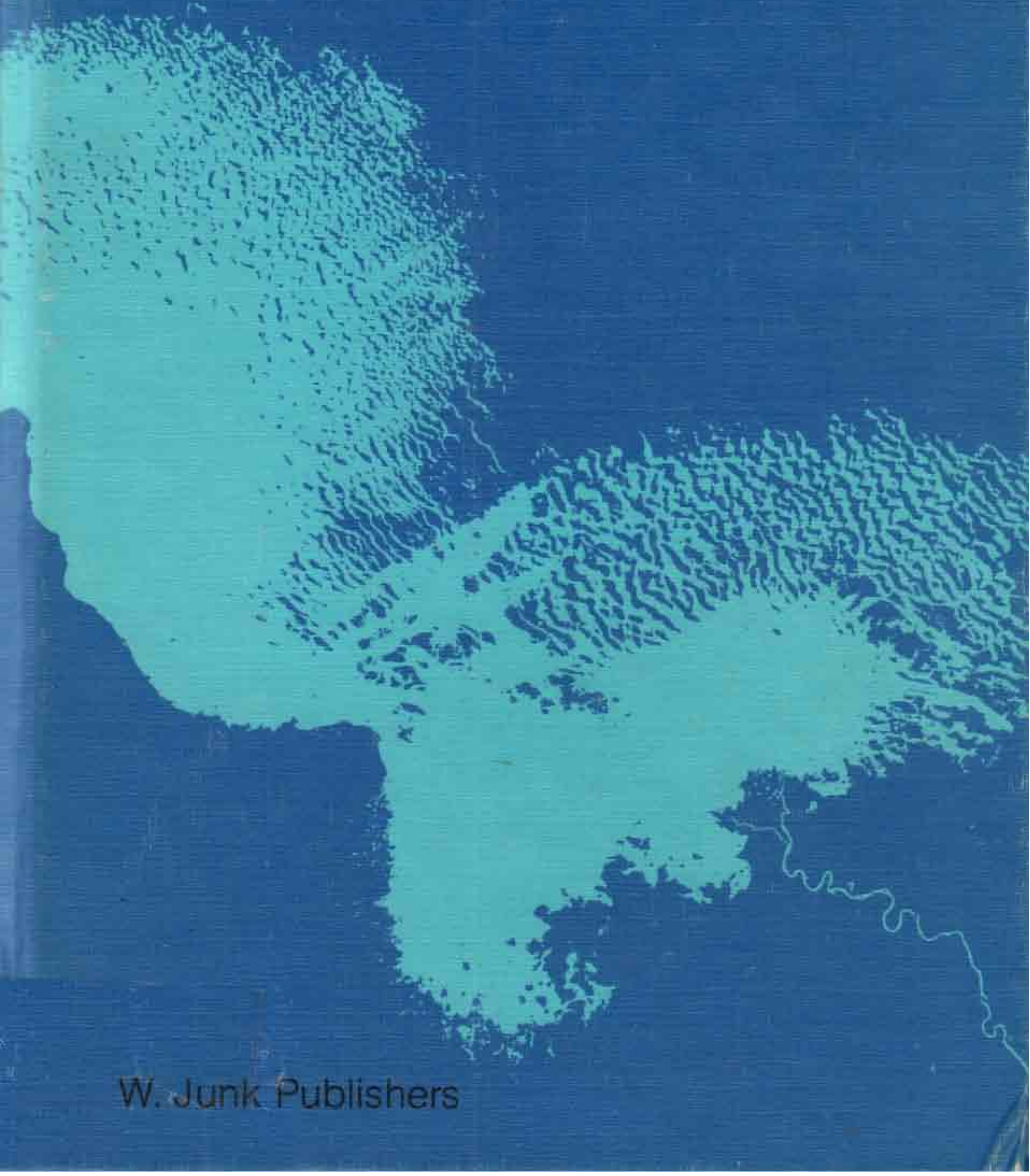

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