12. Secondary production (zooplankton and benthos)

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In order to understand the dynamics of an ecosystem, it is necessary to determine the contribution of the different groups to total biomass as well as to evaluate their turnover rates and the amount of organic matter that each produces per unit time. Therefore, the zooplankton and zoobenthos production were studied as part of the research on the productivity of Lake Chad conducted from 1968 to 1973.

For this purpose, the biology, growth rates and the dynamics of the main species present in the environment which represented a considerable part of the biomass were studied. These different parameters allowed the evaluation of the annual mean production of the different groups and therefore of the biological production of the environment.

12.1 Zooplankton

List of symbols used

D_i = duration of a developmental stage (time interval between the moults which limit the stage)
D_e = duration of the embryonic stage (from laying to hatching)
D_n = duration of the nauplius stage (Copepods)
D_c = duration of the copepodid stage
D_j = duration of the juvenile development of Cladocerans from birth to first laying
D_p = duration of the juvenile development of Copepods ($D_p = D_n + D_c$)
D'_e = time interval between two successive layings
N_E, N_N, N_C, N_A, N_M, N_F, N_T = number of eggs, and embryos, of nauplii, copepodids, adults, males, females and the population (total number)
W, B, P = individual weight, biomass and production
W_i = mean weight of an individual of stage i
W_{iA}, W_A, W_{fA} = initial, mean and final weight of the adults
ΔW_i = increase in weight through stage i

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Z = age expressed as a unit of biological time. These units are equal to the duration of the embryonic stage in days

b = birth rate

12.1.1 *Biological aspects and population structure of the main species*

12.1.1.1 *Reproduction, recruitment and population structure.* The presence of egg-bearing females and juvenile instars in the populations of planktonic copepods throughout the year showed that reproduction and recruitment were continuous. However some variations existed over the year (Fig. 1a). The number of eggs and nauplii of *Tropodiaptomus* decreased to two clearly defined minimum levels (Fig. 1b) corresponding to the cool season (January–February) and to the rainy season (July–August). These minimum levels did not result from a decrease in fecundity since the number of eggs per female (N_E/N_F) remained more or less constant (Fig. 1b) as did the proportion of adults in the population (Fig. 1d). In fact, the minimum levels observed resulted from a decrease in the abundance of adults during these periods.

A rather similar phenomenon was observed in the Cyclopoids but in the cool season the decrease in numbers was less pronounced in *Thermocyclops* which was rare especially during the rainy season (Fig. 1c). The opposite phenomenon occurred in *Mesocyclops*.

According to the available data, it seems that population structures remained fairly stable throughout the period of 'Normal Chad' while considerable changes and above all a big increase in the fecundity of the Calanoids (Table 7) were observed during the drying up of the lake.

Few results are available on variation in fecundity and population structure of the Cladocera, but it can be assumed that they were low, similar to the variations in the ratios N_J/N_T (Table 1) and N_E/N_A (Fig. 2) of the main species. The observations conducted from March 25th to April 24th, 1968 when the temperature increased by 6°C (Fig. 2) show that the fecundity remained rather constant in *Moina* and *Diaphanosoma* and varied in *Daphnia barbata*, according to temperature (decrease of fecundity with temperature increase).

12.1.1.2 *Duration of embryonic development.* The duration of embryonic development (D_e) of the main planktonic crustacean species was determined by laboratory breeding at 24°C (January 1969) and at 29–30° (August 1968 and 1969, July 1973). For three species it was determined by *in situ* breeding at 18–20°C (*Moina micrura*, *Thermocyclops neglectus*, *Mesocyclops leuckarti*) (Gras and Saint-Jean 1969, 1976).

The results obtained are represented by the following sigmoid logistic curve:

$$1/D_e = \frac{K}{1 + e^{b(\hat{\theta} - \theta)}}$$

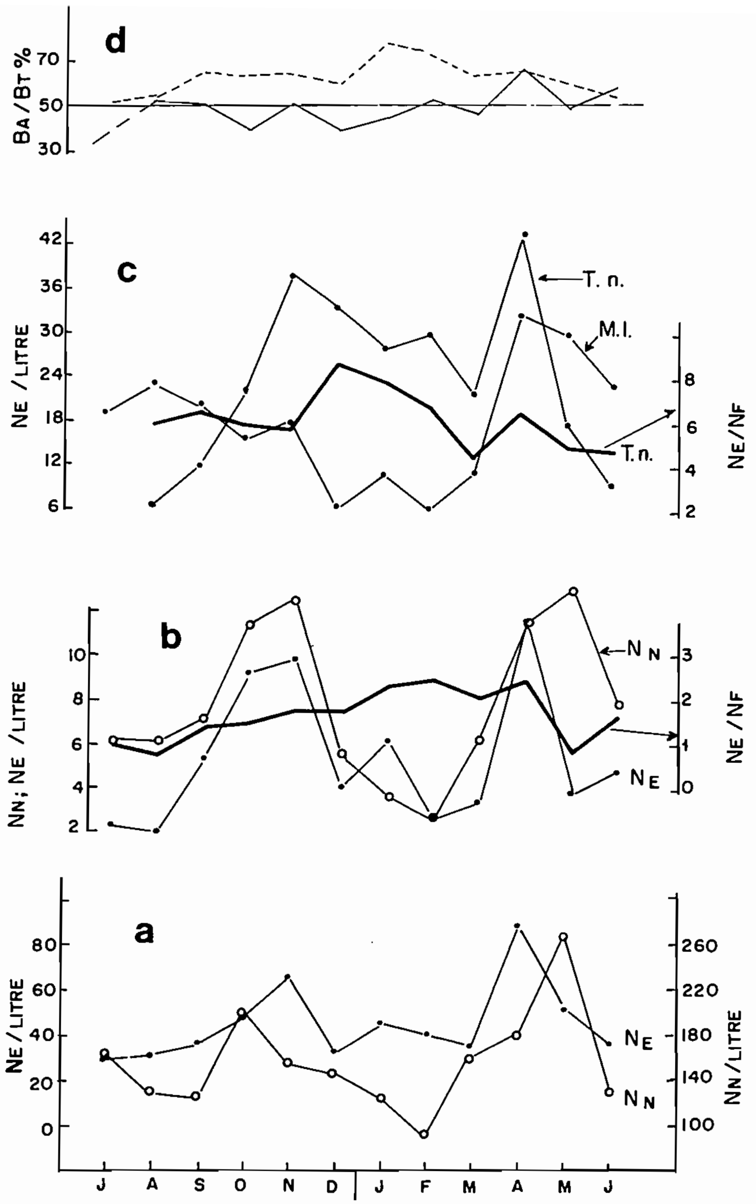

Fig. 1 Variation in the reproduction (number of eggs N_E), fecundity (N_E/N_F), recruitment (number of nauplii N_N) and proportion of adults expressed in terms of weight (B_A/B_T) of Copepods during 1964–1975. (a) Total Copepods, 98% of the nauplii belong to the Cyclopoids on average; (b) Calanoids (*Tropodiaptomus*); (c) Cyclopoids; (d) Cyclopoids (dashes) and Calanoids (lines).

Table 1 Data on zooplankton population structure (percentage of nauplii (N), copepodids (C), adults (A) and young (Y) in relation to the total number) of the main species or groups in the southeastern Archipelago during the period of Normal Chad (1964–1965, 1968) and during the period of 'Lesser Chad' (1973). ‡ = Dominant species; M.m. = *Moina micrura*; D.e. = *Diaphanosoma excisum*; B.l. = *Bosmina longirostris*; D.b. = *Daphnia barbata*; T.i. = *Tropodiaptomus incognitus*; T.g. = *Thermodiaptomus galebi*; T.n. = *Thermocyclops neglectus*; T.i.c. = *Thermodiaptomus incisus circusi*; M.l. = *Mesocyclops leuckarti*.

	CALANOIDS			CYCLOPOIDS			Y(%)					
	N%	C%	A%	N%	C%	A%	Diapt.	Cycl.	M.m	D.e	B.l.	D.b.
1964–65	27	48	25	75	20	5	75	95	–	–	8	–
(annual)	(T.i.‡ + T.g.)			(T.n. + T.i.c. + M.l.)								
1968	58	26	16	–	–	–	84	–	69	72	56	76
(30 days)	(T.i.)											
January 73	21	16	64	62	24	14	37	86	59	63	64	–
(15 days)	(T.i. + T.g.‡)			(T.n. + T.i.c. + M.l.)								
April 73	50	15	35	81	11	8	65	92	59	64	–	–
(15 days)	(T.g.)			(T.n.‡ + M.l.)								

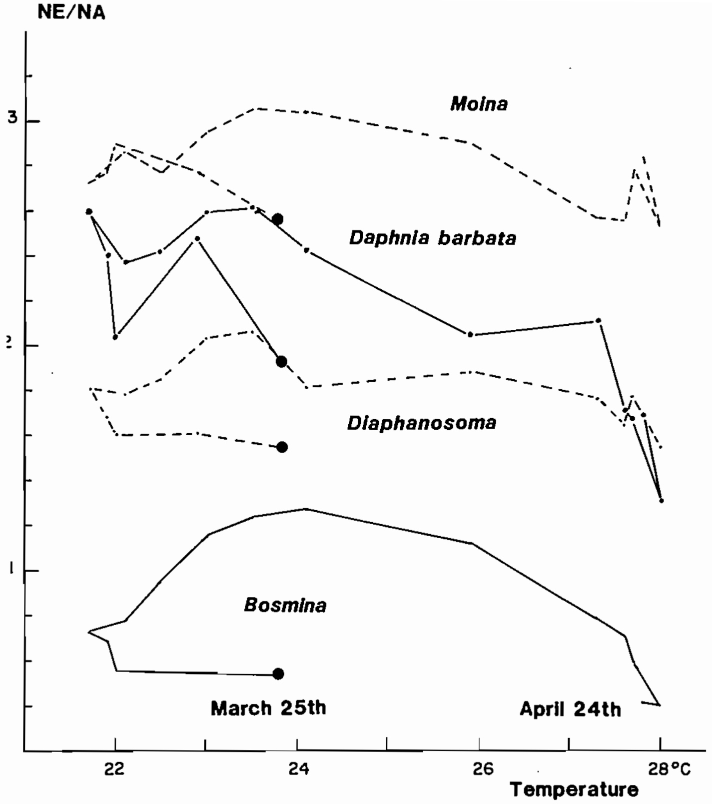

Fig. 2 Variation in the number of eggs per female (N_E/N_A) in relation to the temperature in four species of Cladocera at Melia from March 25th to April 24th, 1968 (Southeastern Archipelago).

It is the model used to describe the variations in the rate of embryonic development ($1/D_e$) in relation to temperature (θ). K is the maximum value $1/D_e$ when temperature increases; $\hat{\theta}$, the optimum temperature of embryonic development is the value of the temperature at the inflection point of the curve; b is a constant (Gras and Saint-Jean 1976).

The median part of the sigmoid curve (Fig. 3) is comparable to a straight line; $1/D_e = 1/S\ (\hat{\theta} - \theta_0)$, where θ_0 is the 'theoretical developmental threshold' and corresponds to the intersection point of the straight line with the x-axis and $1/S$ is the slope of the straight line. The temperature range corresponding to this median part whose approximate limits can be fixed at $\hat{\theta} \pm 6°C$, is generally situated in the optimum development zone according to Winberg (1971) and coincides with the annual temperature range of Lake Chad (19 to 30°C) for most species.

The values of the different parameters of the logistic equation and its

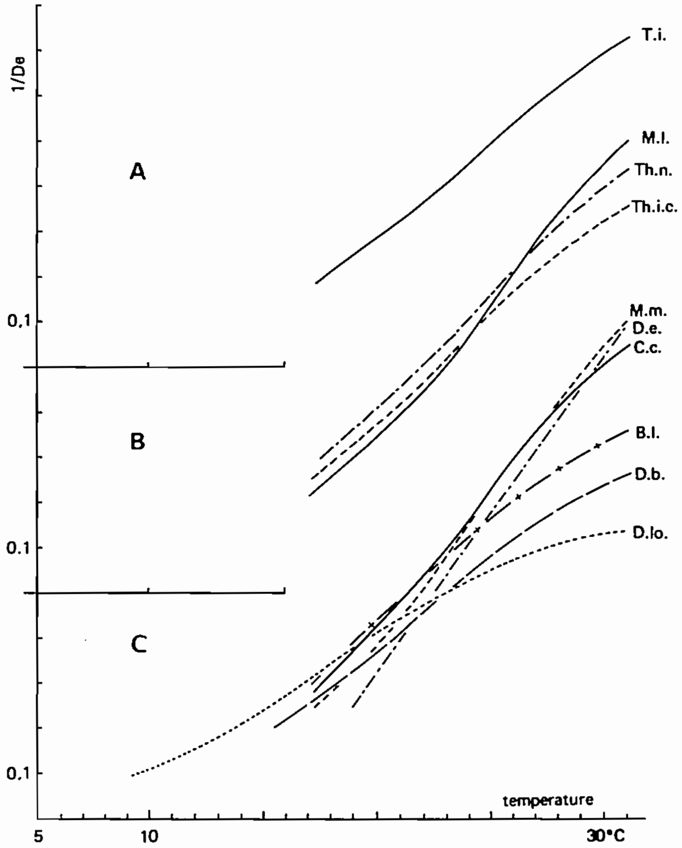

Fig. 3 Embryonic development of the main planktonic crustaceans (logistic curves). T.i. = *Tropodiaptomus incognitus*; M.l. = *Mesocyclops* cf. *leuckarti*; Th.n. = *Thermocyclops neglectus*; Th.i.c. = *Thermodiaptomus incisus circusi*; M.m. = *Moina micrura*; D.e. = *Diaphanosoma excisum*; C.c. = *Ceriodaphnia cornuta*; B.l. = *Bosmina longirostris*; D.b. = *Daphnia barbata*; D.lo. = *Daphnia longispina*.

simplified expression will be found in Table 2 as well as the duration of embryonic development (in hours).

The embryonic development was of similar duration both in the Copepods and the Cladocerans under study; it ranged from 1 to 1.6 days at 30°C, from 1.4 to 2 days at 25°C and from 2.5 to 3 days at 20°C.

The interspecific differences were rather more pronounced at high temperatures. So, at 30°C, three groups could be distinguished:

— species which grew very quickly ($23 < D_e < 25$ h) such as *M. micrura*, *D. excisum*, *C. cornuta* and *M.* cf. *leuckarti*;

— species which grew more slowly ($31 < D_e < 38$ h) such as the three species of *Daphnia*, the two Calanoids and *B. longirostris*;

Table 2 Features of embryonic development of the planktonic crustaceans: parameters of the logistic equation ($\hat{\theta}$, K/2,b) and its linear approximation ($1/D_e = 1/S\ (\theta-\theta_0)$); duration development (D_e) at different temperatures calculated according to the logistic equation (after Gras and Saint-Jean 1976.)

Species	$1/D_e = 1/S\ (\theta-\theta_0)$ (in days)	$\hat{\theta}$	K/2	b	D_e (hours)		
					20	25	30°C
B. longirostris	0.0452 $(\theta-10.5)$	21.0	0.475	0.21	56	36	29
D. longispina	0.0309 $(\theta-6.9)$	18.4	0.355	0.19	59	43	37.5
D. barbata	0.0391 $(\theta-10.4)$	22.0	0.455	0.19	65.5	41.5	32.5
D. lumholtzi	0.0328 $(\theta-9.0)$	21.2	0.40	0.18	67	45	36
C. affinis							28.5
C. cornuta	0.058 $(\theta-12.7)$	23.7	0.64	0.20	58	33	24
M. micrura dubia	0.0656 $(\theta-14.1)$	24.6	0.69	0.21	63	33.5	23
D. excisum	0.0685 $(\theta-15.1)$	25.3	0.70	0.21	69.5	35.5	23.5
T. incognitus	0.0406 $(\theta-13.1)$	24.1	0.445	0.20	88	49.5	35
T. incisus circusi	0.0461 $(\theta-12.0)$	23.0	0.505	0.20	67	40	29.5
T. neglectus	0.0476 $(\theta-11.7)$	24.3	0.60	1.175	62.5	38	27.5
M. cf. *Leuckarti*	0.0595 $(\theta-14.4)$	25.4	0.655	0.20	72	38	25.5
T. galebi							33.5

— species with intermediate features such as *T. incisus circusi* and *T. neglectus*. The second species had developmental features similar to those of *Thermocyclops hyalinus consimilis* found at Lake George (Burgis 1971).

Below 20°C, the previous classification was reversed since *B. longirostris* and *D. longispina* had the most rapid growth. These two species whose optimum temperature of embryonic development were lower (Table 2) are cosmopolitan forms that were well represented in the temperate zone and prevailed in Lake Chad during the cool season. On the contrary, the other Cladocera species with a higher optimum developmental temperature and whose optimum zone had shifted towards high temperatures, were more abundant in the warm season (cf. Gras and Saint-Jean 1976).

Moreover, it was observed during experiments that the duration of embryonic development of the Copepods *M. leuckarti* and *T. neglectus* decreased by about 10% in July 1973 at 30°C, compared with August 1968. This difference can be accounted for by the influence of nutritional conditions.

12.1.1.3 *Duration of juvenile development*

— Cladocera

The duration of juvenile development (D_j) was also determined in the laboratory at 29–30°C (August 1968) and at 24°C (January 1969) (Gras and

Saint-Jean 1969, 1978). The mean duration of juvenile development (D_j) of the species studied at 25 and 30°C will be found in Table 3 as well as the duration of the cycle, egg to egg ($D_j + D_e$). It also shows the relative duration of juvenile development (D_jD_e) which is the ratio between the duration of juvenile development at the temperature, θ, and the duration of embryonic development at the same temperature. This ratio D_j/D_e did not vary much at 25°C and 30°C.

Roughly the same groups of species as previously identified for embryonic development were found again. The first one was composed of *M. micrura*, *D. excisum* and *C. cornuta* which had rapid embryonic and juvenile development, the cycle from egg to egg ranging from 73 to 110 h at 25°C, and from 52 to 81 h at 30°C. The second one corresponded to the three species of *Daphnia* whose cycle ranged from 165 to 198 h at 25°C. *B. longirostris* appeared to occupy an intermediate position.

M. micura was characterized by a very rapid juvenile development whose duration barely exceeded the duration of embryonic development ($D_j/D_e = 1.2$). The ratios D_j/D_e which were much higher in *Daphnia* can be compared to those obtained for *Daphnia* species under temperate conditions.

The number of juvenile stages varied with the individuals under laboratory conditions. Generally, it is 2 or 3 in *M. micrura*, 4 in *C. cornuta* and *C. affinis*, 5 in *D. lumholtzi*, 4 to 6 in *D. barbata* and *D. excisum*.

In the natural environment, the evaluation of the number of juvenile stages according to the size structure of the population showed that there were some modifications from 1968 to 1973. So, 3 to 4 stages were observed in *M. micrura* in 1968, 2 to 3 in 1972 and 2 in the Eastern Archipelago in 1973; and 5 to 6

Table 3 Cladocera: mean duration of juvenile development (D_j); relative duration in relation to the duration of embryonic development (D_j/D_e) and duration of the cycle from egg to egg (after Gras and Saint-Jean 1978).

Species	25°C (January 1969)			30°C (August 1968)		
	D_j (hours)	D_j/D_e	Duration of cycle (hours)	D_j (hours)	D_j/D_e	Duration of cycle (hours)
Bosmina longirostris	86.8	2.37	123.8	70.0	2.57	
Daphnia longispina	154.5	3.60	198.5			
Daphnia barbata	132.0	3.14	173.5	102.1	3.26	
Daphnia lumholtzi	120.3	2.63	165.3	104.9	3.01	
Ceriodaphnia affinis					1.97	
Ceriodaphnia cornuta	60.6	1.80	99.6	47.4	1.98	81.4
Moina micrura	40.2	1.20	73.4	28.9	1.26	51.9
Diaphanosoma excisum	75.4	2.13	110.9	54.6	2.32	78.1

stages were observed in *D. excisum* in the same region in 1968, 5 in 1972 and 4 in 1973.

+ Copepods

The results obtained from 4 sets of observations are listed in Table 4. Calanoids and Cyclopoids had a juvenile development (D_p/D_e) identical in duration for a given year: 12.6 to 17.3 in *T. incognitus* and about 18.5 in *T. neglectus* and *M.* cf. *leuckarti* in 1968–69; 7.7 in *T. galebi* and about 6 in *T. neglectus* and *M.* cf. *leuckarti* in 1973. These durations were much longer than those of the Cladocera where D_j/D_e ranged from 1.2 to 3.6. However, it can be pointed out that the values observed in 1973 were much lower than those observed in the Cyclopoids in 1968–69.

The durations of the Copepodid (D_c) and nauplius (D_n) stages were roughly identical in the Cyclopoids ($D_c/D_n \simeq 1$) but very different in the two Calanoids studied: $D_c/D_n \simeq 4.5$ in *T. incognitus* and 2 in *T. galebi*. The different copepodid stages did not have the same duration in the four species; the first three stages were shorter than the following ones while stage C5 was the longest.

12.1.1.4 *Time interval between two layings.* In Cladocera, the emergence of the young from an egg by incubation often occurs just before the moult and subsequent egg-laying so that the time interval between two layings (D'_e) is roughly equal to the duration of the embryonic development (D_e).

In Lake Chad, the interval between hatching and laying, as estimated in culture, was 20 minutes for *D. excisum*, *C. cornuta*, *C. affinis* and *M. micrura*, 1 h for *D. longispina* and *D. humholtzi*, 3 h for *D. barbata* and 4 h for *B. longirostris*.

In the Copepods, D'_e was much higher than D_e, the mean values of D'_e/D_e ranging from 1.5 to 2.4 in 1968 and 1969 (Table 5) (Gras and Saint-Jean 1976). On the contrary, in 1973, this time interval could be compared to that of the Cladocera (a few hours) probably because of the improved nutritional conditions of the natural environment.

12.1.1.5 *Growth of the Copepods.* Growth expressed as weight was determined for the main species after evaluating the weight, W_i, and the duration, D_i, of the stages at 30°C (Gras and Saint-Jean 1979). The results of the observations conducted on *T. incognitus* in August 1969 and on *T. galebi*, *T. neglectus* and *M. leuckarti* in July 1973 are listed in Table 6 as weight of the different stages (W_i), duration of these stages and daily increase in weight $\Delta W_i/D_i$).

The growth curves corresponding to the above-mentioned experimental data were determined by expressing the duration of embryonic development as a unit of time (or of age) (Fig. 4). In the four species under study, it was estimated that growth was exponential during the nauplius stage. It remained so during the copepodid stage of the Cyclopoids *M.* cf. *leuckarti* and *T. neglectus*, while it assumed a parabolic shape during the copepodid stage of the Calanoids, *T. galebi* and *T. incognitus*.

Table 4 Mean instar duration (days) in Copepods; D_e = embryonic development; D_n = duration of the nauplius stage; D_c = duration of the copepodid stage; D_p = duration of juvenile development ($D_c + D_n$); D_c1 to D_c5 = duration of the five copepodid stages (after Gras and Saint-Jean).

Species	Dates	Temperature	D_e	D_n	D_c1	D_c2	D_c3	D_c4	D_c5	D_c	D_p
Thermocyclops	01/69	24°	1.71	16.00	← 11.0 →				4.5	15.50	31.50
neglectus	07/73	30°	1.01	2.93	0.57	0.52	0.51	0.60	0.86	3.06	5.99
Mesocyclops cf.	01/69	24°	1.77	18.00	← 9.5 →			← 5.5 →		15.00	33.00
leuckarti	07/73	30°	0.96	2.66	0.48	0.45	0.48	0.64	0.87	2.92	5.58
Tropodiaptomus incognitus	01/69	24°	2.25	6.50	← 20.10 →				10.40	30.50	37.00
	08/68	30°	1.45	3.20	← 10.00 →				5.00	15.00	18.20
	08/69	30°	1.47	4.84	2.18	2.45	3.50	5.70	6.80	20.63	25.47
Thermodiaptomus galebi	07/73	30°	1.40	3.45	0.99	0.97	1.08	1.83	2.50	7.37	10.82

Table 5 Time interval between two successive layings (D'_e) in Copepods. Values observed in laboratory during January 1969 and August 1968. The range values are mentioned in brackets (after Gras and Saint-Jean 1976).

Species	1969 January (24–25°C)		1968 August (29–30°C)	
	D'_e (hours)	D'_e/D_e	D'_e (hours)	D'_e/D_e
T. incognitus	99 (63–109)	2	53 (46–77)	1.5
M. cf. *leuckarti*	57 (47–64)	1.5	38 (30–40)	1.5
Th. neglectus	62 (44–86)	1.5	54 (41; 46; 76)	2
Th. incisus circusi	90 (73–109)	2.2	72 (45–95)	2.4

Therefore, the growth equations for the copepodid stages are as follows:
Cyclopoids *M.* cf. *leuckarti*: $W = 0.155\ e^{1.086(Z-2.77)}$
T. neglectus: $W = 0.155\ e^{0.866(Z-2.9)}$

Z is the age expressed in units equal to the duration of embryonic development, D_e (in days); $Z = 0$ at birth, $2.77 = D_n/D_e$ of *M. leuckarti* and $2.9 = D_n/D_e$ of *T. neglectus*. The value 0.155 correspond to the initial weight (in µg) of the Copepodids *M. leuckarti* and *T. neglectus*.

Calanoids *T. galebi*: $W = 0.247\ (Z - 1.06)^{2.1}$
T. incognitus: $W = 0.249\ (Z - 1.5)^{1.3}$

Given a temperature other than 30°C and the same value for D_p/D_e, the daily increases in weight were calculated after evaluating D_i at this temperature. For this evaluation it was assumed that the relative duration, D_i/D_e, of the stages remains constant and knowing D_e from the laws of variation of D_e previously determined in relation to the temperature. Insofar as the D_i/D_e are assumed to be constant, the shape of the curve does not change regardless of temperature (Gras and Saint-Jean 1981).

12.1.1.6 *Conclusions.* The laboratory observations showed a very great acceleration in juvenile development of the Cyclopoids from 1969 to 1973. The ratio D_p/D_e as well as the relative duration of the nauplius (D_n/D_e) and copepodid (D_c/D_e) stages decrease by about three times between the two above-mentioned sets of observations.

In the Calanoids, although the comparison seems to be less convincing because the species studied over the two periods were not the same, it also appears that there was an acceleration of development. The relative duration of the development observed in 1973 ($D_p/D_e = 7.7$) for *Thermodiaptomus* was, in fact, much shorter than the lowest value observed for *Tropodiaptomus* (12.6) in 1968–69. A more justified comparison can be made if the copepodid stages only

Table 6 Planktonic copepods: mean dry weight of an individual ($\overline{W}_i$ in μg) for each stage; absolute duration of these stages (D_i in days) and daily increase in weight ($\Delta W_i/D_i$); E = embryonal stage; N = nauplius stage; C1 to C5 = copepodid stages; Ac = adults in growth; A = adult. Results obtained in August 1969 for *T. incognitus* and in July 1973 for the other species (after Gras and Saint-Jean).

	Tropodiaptomus incognitus			*Thermodiaptomus galebi*			*Thermocyclops neglectus*			*Mesocyclops* cf. *leuckarti*		
	$\overline{W}_i$ (µg)	D_i (days)	$\Delta W_i/D_i$	$\overline{W}_i$ (µg)	D_i (days)	$\Delta W_i/D_i$	$\overline{W}_i$ (µg)	D_i (days)	$\Delta W_i/D_i$	$\overline{W}_i$ (µg)	D_i (days)	$\Delta W_i/D_i$
E	0.20	1.47	0	0.08	1.40		0.015	1.01		0.015	0.96	
N	0.40	4.84	0.09	0.25	3.45	0.15	0.05	2.93	0.05	0.05	2.66	0.05
C1	0.85	2.18	0.23	0.85	0.99	0.59	0.20	0.57	0.17	0.20	0.48	0.23
C2	1.50	2.45	0.34	1.50	0.97	0.99	0.30	0.52	0.27	0.35	0.45	0.40
C3	2.70	3.50	0.38	2.85	1.08	1.32	0.50	0.51	0.42	0.60	0.48	0.67
C4	4.60	5.70	0.43	5.30	1.83	1.81	0.85	0.60	0.67	1.10	0.64	1.28
C5	7.30	6.80	0.48	9.70	2.50	2.55	1.35	0.86	1.27	2.35	0.87	3.07
Ac		4.38	0.52		1.41	3.25						
A	11.00			17.40			2.15			4.55		

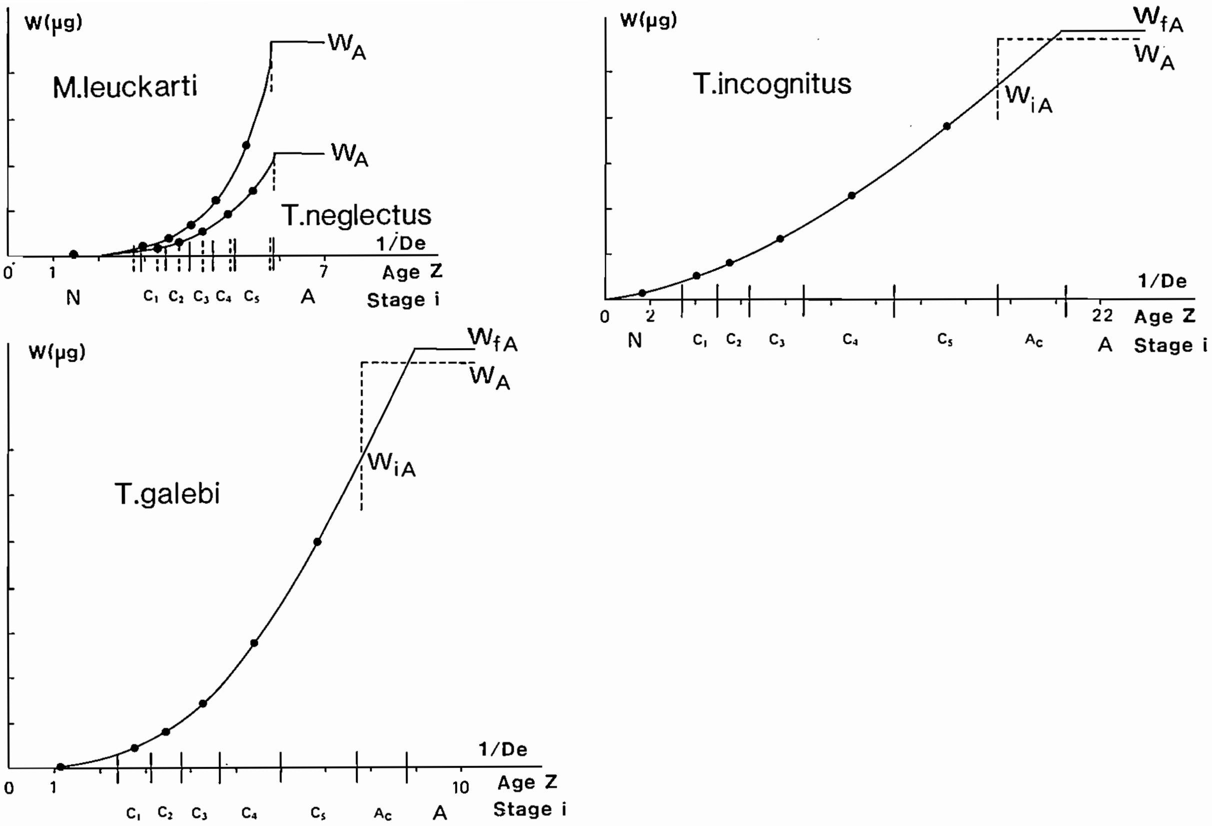

Fig. 4 Growth in dry weight for four species of Copepods. In the range of ages, the unit is equal to $1/D_e$ (D_e, in days), W_A = mean weight of adults; W_{iA} and W_{fA} = initial and final weight of adults; N = nauplii; C_1–C_5 = copepodid stages; Ac = adults in growth; A = adults reaching the end of their growth.

of each species are considered. The value of 5.3 and 10.4 respectively are even more different (Gras and Saint-Jean 1981).

With a simultaneous analysis of the conditions of the natural populations and, above all, a comparison between the populations sampled at Melia in March–April, 1968 and those sampled at Tchongolerom in 1972–1973, significant modifications seem to be revealed which are in keeping with the previous acceleration of development. A reduction in the number of juvenile stages was observed in the two main species of Cladocera, *M. micrura* and *D. excisum*, probably along with a decrease in the duration of juvenile development. So, for *M. micrura* D_j/D_e would move from 1.8 in 1968 to 0.7 in 1973 and for *D. excisum* from 3.2 to 1.6 (Gras and Saint-Jean 1978).

Moreover, there was an increase in clutch size in all the filtering or mixed diet species (Table 7). A reduction in the time interval between layings could also be noted in the Cyclopoids from the laboratory observations of 1973. All these modifications of biological parameters could have resulted from an improvement in nutritional conditions following an increase in the algal biomass per unit volume during the drying up period of the lake (Iltis 1977).

During 1973, from the population point of view, there was an increase in the proportion of adult Copepods as well as the Cladocerans, *M. micrura* and *D. excisum*. The above-mentioned modifications of decrease in D_j/D_e, and increase in the size of layings account for this. This phenomenon may occur along with an increase in the birth rate (Gras and Saint-Jean 1978).

12.1.2 *Evaluation of production*

12.1.2.1 *Methods.* In Cladocera, production was calculated from the formula: $P = bB$ where B is the biomass expressed in mg of dry weight per m^3, and b is the birth rate of the population expressed by the relation:

$$b = \frac{1}{D_e} \ln\left(1 + \frac{N_E}{N_T}\right)$$

D_e being the duration expressed in days of the embryonic development and N_E/N_T the ratio between the number of embryos (N_E) and total free individuals (N_T), found in the sample of the population considered.

In Copepods, the formula is:

$$\underbrace{\sum \frac{\Delta W_i}{D_i} . N_i}_{\text{Production of the nauplius and copepodid stages}} \quad + \quad \underbrace{\frac{W_E . N_E}{D_e}}_{\text{Production of adults in the form of eggs}}$$

Table 7 Size of the layings (number of eggs/number of egg-bearing females) in the main species of planktonic crustaceans during the period of Normal Chad (1964–65 and 1968) and during the period before the drying up (1972–73) in the different stations of the eastern archipelago. For the years 1964–65, it is the average obtained in the five stations sampled each month. In 1968, it is the average of 16 samples taken in March–April. In 1972 and 1973, it is the average of 2 to 8 samples (after Gras and Saint-Jean).

	Archipelago	Melia	Tchongolerom					Tchongolerom–Melia			
Dates	1964–65	1968	May 1972	June 1972	August 1972	January 1973	March 1973	June 1972	August 1972	January 1973	March 1973
Tropodiaptomus incognitus	3.8	3.5	6.8	7.0	5.9	9.3	–	8.0	3.2	7.5	–
Thermodiaptomus galebi	9.1	5.0	12.1	11.9	11.8	22.0	27.8	15.2	9.8	16.9	29.1
Thermocyclops neglectus	15.3	–	14.0	16.4	18.0	22.7	23.3	–	13.8	16.2	24.7
Mesocyclops leuckarti	42.0	–	44.9	37.7	37.2	34.4	45.0	–	36.6	47.7	42.4
Moina micrura dubia	–	3.2	4.0	4.0	4.5	6.4	5.7	4.9	3.6	3.9	5.3
Diaphanosoma excisum	–	2.1	2.3	2.6	2.9	3.2	3.1	3.3	2.6	3.0	3.8
Bosimina longirostris	–	1.0	1.9	1.7	–	3.4	–	–	8	3.1	–

ΔW_i is the increase in weight during the stage i with a duration D_i and a number N_i, W_E is the weight of eggs with the number N_E.

12.1.2.2 *Results.* The daily production and the daily production rate ($P/\bar{B}$) were calculated from samples taken over several days and at different times (and temperatures) at three stations situated in the Eastern Archipelago of the lake (Table 8).

It should be noted that the production rate varied considerably with species, the greatest difference being observed in January 1973 when the production rate of *Moina* was 20 (Tchongolerom) or 27 times (Tchongolerom–Melia) higher than that of the Calanoids. The classification of the species according to decreasing production rate is:

1. *Moina*	$0.27 < P/\bar{B} < 0.87$
2. *Diaphanosoma* *Bosmina* *Daphnia*	$0.16 < P/\bar{B} < 0.50$
3. Cyclopoids	$0.10 < P/\bar{B} < 0.27$
4. Calanoids	$0.01 < P/\bar{B} < 0.07$

On the other hand, the distribution of production between the different developmental instars was irregular as shown by the biomass distribution and the variations in production rate according to the stages (Table 9). Given their low production rate (ranging from 0.003 to 0.033), the adult Copepods which represented a high percentage of the biomass, thus represented only a small percentage of the production of their populations (20 to 50% for Calanoids and 5 to 10% for Cyclopoids). These distributions, especially in the Calanoids, showed great variability which can be accounted for (Gras and Saint-Jean, in preparation). The analysis of distribution of the five copepodid stages revealed a sharp difference between *Mecocyclops* cf. *leuckarti* and *Thermocyclops neglectus*. The first 2–3 stages contributing a higher percentage of production in *Mesocyclops* (Fig. 5) because of their greater abundance. In order to make them independent of temperature, production and production rate are expressed as D_e, the duration of embryonic development (in the case of monospecific populations) or U, a unit combining the D_e values of species comprising the community, as a function of time.

This expression shows (Fig. 6) that the production rate of the population remained rather similar in the different series of observations ranging from 0.18 (at Tchongolerom in May, 1972) to 0.38 (at Tchongolerom-Melia in March, 1973). The main cause of variation in this rate was the respective abundance of the Calanoids (minimum production rate) and the Cladocera, especially *Moina* (maximum rate).

The production of the crustacean populations was also estimated over a year during the period of high water in the Eastern Archipelago (1964–65) and for

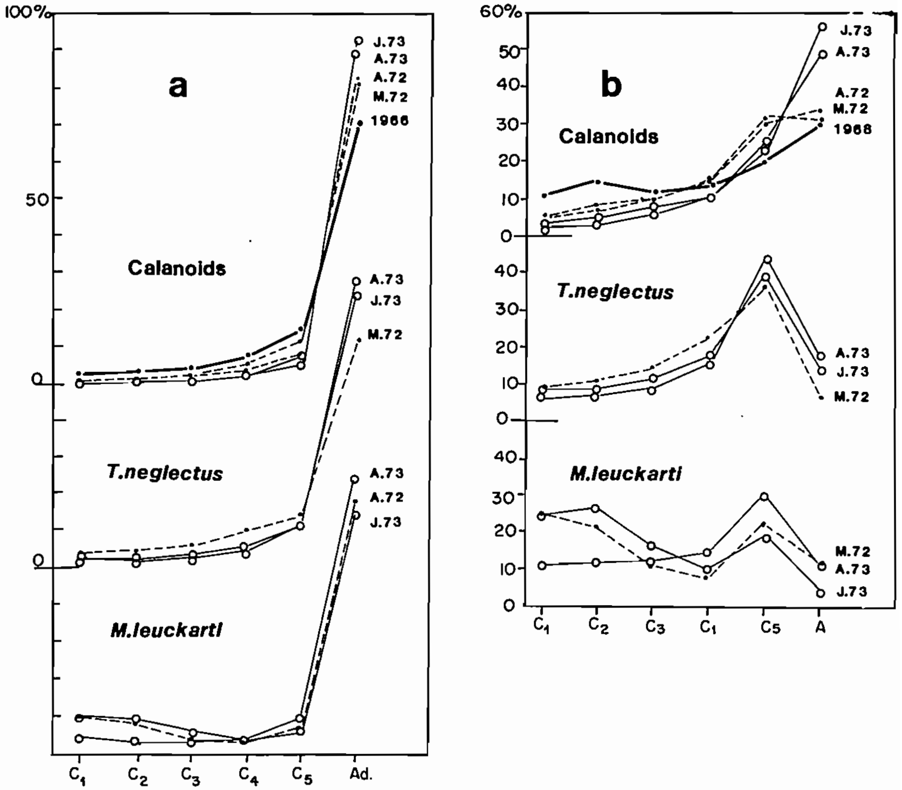

Fig. 5 Distribution of the biomasses (a) and production (b) according to the developmental instars in Copepods during 1968 and in the series of May (M) August (A) 1972 and, January–February (J) and March–April (A) 1973 at Tchongolerom (Eastern Archipelago).

the whole lake in the cold season (February–March 1971), with the production rates observed at Melia in March–April 1968 (Tables 10 and 11).

In the three large groups, the Cladocera, Calanoids and Cyclopoids as well as the total community (Fig. 7), the production rates were naturally at minimum level during the cold season. The variation was regular and rather low in amplitude over the year, the ratio between maximum and minimum values only reaching 2.45 (0.27/0.11). Moreover, spatial distribution was not very heterogeneous if each main region is considered individually like the distribution in biomasses observed in 1971. Production rates were of equal value everywhere, but the production (per m^3) was much lower in the Southern Open Water than in the rest of the lake (Table 11) (as was biomass).

If the annual community production rate observed at a mean temperature of 26.2°C, that is to say 63.7 (Table 10) during 1964–65, is applied to the biomass

Table 8 Mean biomass, $\bar{B}$, (in mg dry weight per m^3), mean daily production, P_j (in mg dry weight per m^3) and daily P/$\bar{B}$ ratio of zooplankton in three stations of the Eastern Archipelago during different periods. M.m. = *Moina micrura*; D.e. = *Diaphanosoma excisum*; B.l. = *Bosmina longirostris*; D. = *Daphnia.*

	Date	Mean temperature (in °C)		Cladocera				Cladocera (total)	Calanoids (total)	Cyclopoids (total)	Total
				M.m	D.e.	B.l.	D.				
Melia	March-	24.5	$\bar{B}$	22.8	18.6	90.0	9.7	141.1	185.5	65.4	392.0
	April		P_j	10.8	5.3	18.3	2.0	36.4	13.1	7.3	56.8
			P/B	0.47	0.28	0.20	0.21	0.26	0.07	0.11	0.15
Tchongolerom	May	29.5	$\bar{B}$	17.4	30.8	3.4	0	51.6	236.0	77.3	364.9
	1972		P_j	12.0	9.1	1.2		22.3	17.1	16.9	55.4
			P/B	0.69	0.30	0.34		0.43	0.07	0.22	0.15
	June	30.4	$\bar{B}$	17.9	29.6	0.3	0	47.8	149.4	40.9	238.1
	1972		P_j	16.3	14.7	0.1		31.1	10.5	9.5	51.1
			P/B	0.86	0.50	0.35		0.64	0.07	0.23	0.21
	August	28.6	$\bar{B}$	28.5	34.3	ε	0	62.8	142.2	16.3	221.3
	1972		P_j	22.9	16.3	–		39.2	9.9	4.0	53.1
			P/B	0.80	0.48	–	–	0.63	0.07	0.24	0.24
	January-	19.1	$\bar{B}$	10.5	4.2	2.0	0	16.7	139.3	43.6	199.6
	February		P_j	4.2	0.8	0.5		5.5	2.7	4.3	12.5
	1973		P/B	0.40	0.19	0.26		0.33	0.02	0.10	0.06
	March-	25.6	$\bar{B}$	6.1	3.3	0	0	9.4	58.2	178.6	246.2
	April		P_j	5.3	1.3			6.6	3.1	35.7	45.4
	1973		P/B	0.87	0.41			0.70	0.05	0.20	0.18

Tchongolerom-Melia	August 1972	28.6	$\bar{B}$	22.9	30.4	ε	3.6	56.9	99.5	21.7	178.1
			P_j	14.7	12.0		1.2	27.9	6.0	5.6	39.5
			$\overline{P/B}$	0.64	0.40		0.33	0.49	0.06	0.26	0.22
	January-February 1973	19.1	$\bar{B}$	26.7	3.6	5.1	0	35.4	75.6	101.3	212.3
			P_j	7.3	0.6	1.1		9.0	0.8	12.9	22.7
			$\overline{P/B}$	0.27	0.16	0.21		0.25	0.01	0.13	0.11
	March-April 1973	25.6	$\bar{B}$	42.1	10.2	0	0.3	52.6	112.0	245.9	410.5
			P_j	28.3	3.2			31.5	6.7	60.6	98.8
			$\overline{P/B}$	0.67	0.31			0.60	0.06	0.25	0.24

Table 9 Distribution of the production and biomass between the nauplii (N), the Copepodids (C) and the adults (A) of Calanoids and Cyclopoids in the populations sampled during 1968, 1972 and 1973 in the stations of the Eastern Archipelago of Lake Chad. The production is expressed as mg m^{-3} per unit of biological time. P_{AE} is the adult production in the form of eggs. In the Cyclopoids, $P_A = P_{AE}$; in the Calanoids, P_{AE} must be added with a term corresponding to a production by increase in body weight.

	Date	Calanoids					Cyclopoids			
		P_N (% P_T)	P_C (%)	P_A (%)	P_{AE} (mg)	P_T (mg)	P_N (% P_T)	P_C (%)	P_{AE} (%)	P_T (mg)
		B_N (% B_T)	B_C (%)	B_A (%)		B_T (mg)	B_N (% B_T)	B_C (%)	B_A (%)	B_T (mg)
Melia	March-April	29.9	49.5	20.7		25.9		88.6[a]	11.3[a]	
	1968	8.5	27.8	63.7	2.2	185.5		16.3	40.9	
	($n = 16$)									
Tchongolerom	May	13.4	59.6	27.0		25.5	26.9	67.3	5.8	19.6
	1972	2.2	19.7	78.1	3.0	236.0	13.2	31.2	55.6	77.3
	($n = 5$)									
	June	18.7	49.9	31.4		15.0	30.3	61.8	7.9	10.4
	1972	2.8	14.4	82.8	2.1	149.4	15.7	27.4	56.9	40.9
	($n = 2$)									
	August	17.8	54.7	27.4		15.6				
	1972	2.3	18.2	79.5	2.1	142.2				
	($n = 5$)									
	January-February	2.7	42.7	54.6		11.1	13.4	75.0	11.6	12.4
	1973	0.3	7.5	92.2	4.3	139.3	4.8	23.9	71.3	43.6
	($n = 8$)									
	March-April	9.5	46.3	44.2		6.2	33.1	55.7	11.2	55.2
	1973	1.2	10.7	88.1	1.6	58.2	12.8	19.4	67.8	178.6
	($n = 8$)									

Tchongolerom-Melia	August	12.2	69.8	18.0		9.7				
	1972	2.1	29.9	68.0	0.7	99.5				
	($n=5$)									
	January-February	18	50.0	32.0		2.5	18.7	78.0	3.3	3.3
	1973	0.8	5.7	93.5	0.4	75.6	8.6	31.9	59.5	101.3
	($n=8$)									
	March-April	18.5	39.2	42.3		14.5	36.4	57.2	6.4	97.2
	1973	2.9	10.8	86.3	4.2	112.0	14.8	24.3	60.9	245.9
	($n=8$)									

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[a] % of P_C+P_N or B_C+B_A.

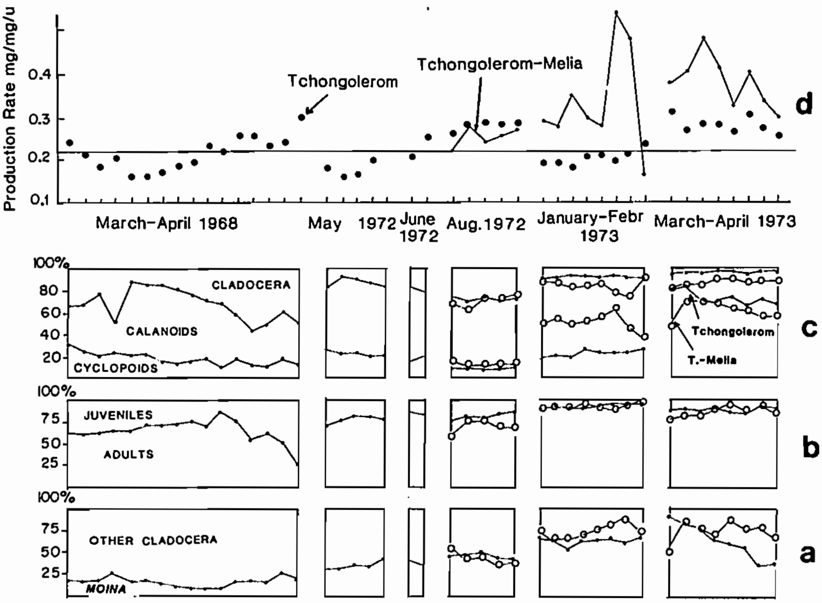

Fig. 6 Variations in the different series of samples during 1968, 1972 and 1973; (a) in the proportion of *Moina* in relation to the other Cladocerans; (b) in the proportions of young and adults expressed in terms of weight in the calanoid populations; (c) in proportions of Cladocerans, Cyclopoids and Calanoids; (d) in the production rate of the population per unit of biological time (unit designated by U which is, in each series, a weighted average of the values of the duration in the embryonic stage of the species belonging to the population).

values observed in 1971, the three major natural regions of the lake had the following production values:

— 567 kg ha^{-1} $year^{-1}$ (dry weight) for the Northern basin;
— 440 kg ha^{-1} $year^{-1}$ for the Southern Archipelago and the Great Barrier;
— 159 kg ha^{-1} $year^{-1}$ for the Southern Open Water.

The annual production can be estimated as 780 000 tons dry weight, or an average of 433 kg ha^{-1} during the period of 'Normal Chad', for the whole lake (about 18 000 km^2).

There are only a few studies of zooplankton production in tropical Africa. Burgis (1971) quotes daily production rates for *Thermocyclops hyalinus* in Lake George ranging from 0.08 to 0.26 according to the method of calculation used. The first value which seems to be retained by the author is considerably lower than that of 0.17 which was calculated for Cyclopoids in Lake Chad during 1964–1965 at a mean temperature of 26.3°C similar to that recorded in Lake George (25 to 26°C). In Lake Turkuna (Ferguson 1975), the production rate N_E/N_T. De for *Tropodiaptomus banforanus* ranging from 0.04 to 0.56 is considerably higher than those calculated for Calanoids in Lake Chad since the latter

Table 10 Monthly values of the daily production, biomass and the production rate in the central zone of the Archipelago in the south basin during 1964–1965 (averages of 5 stations).

Months		1964						1965						P annual (mg m^{-3})	$\bar{B}$	P/$\bar{B}$ annual
		07	08	09	10	11	12	01	02	03	04	05	06			
Moina micrura	P_j	13.9	9.1	10.2	5.3	9.3	4.4	2.4	3.2	6.1	20.4	11.7	2.5	3148.1	16.5	190.8
Diaphanosoma excisum	P_j	5.5	6.4	15.3	10.9	13.1	3.9	1.3	1.7	8.1	11.0	18.7	10.7	3242.4	27.5	117.9
Bosmina longirostris	P_j	5.7	3.4	1.6	6.7	7.2	3.6	5.7	10.5	5.3	11.4	5.4	3.3	2123.1	29.6	71.7
Daphnia	P_j	0.2	1.3	1.5	4.9	5.9	6.2	10.2	16.2	10.2	10.7	1.4	0.4	2101.8	27.8	75.6
Ceriodaphnia	P_j	19.1	15.2	11.8	13.9	4.9	9.9	3.4	1.4	1.1	15.1	11.8	7.3	3494.9	23.1	151.3
Cladocera	$\bar{B}$	99.7	84.7	94.1	114.1	137.0	126.5	136.2	182.5	122.2	199.1	130.5	67.5		124.5	
(total)	P_j	44.4	35.4	40.4	41.7	40.4	28.0	23.0	33.0	30.8	68.6	49.0	29.2	14 110.3		
	P/$\bar{B}$	0.44	0.42	0.43	0.37	0.29	0.22	0.17	0.18	0.25	0.34	0.38	0.43			113.3
Calanoids	$\bar{B}$	101.4	110.8	138.6	220.3	224.1	108.1	83.7	60.6	118.1	238.0	273.2	145.6		151.9	
(total)	P	9.2	8.6	9.7	15.2	13.3	4.3	2.3	2.0	6.4	14.3	17.7	12.2	3504.0		
	P/$\bar{B}$	0.09	0.08	0.07	0.07	0.06	0.04	0.03	0.03	0.05	0.06	0.07	0.08			23.1
Cyclopoids	$\bar{B}$	41.0	39.2	44.9	55.9	79.6	41.3	58.7	53.6	73.6	77.4	73.4	38.4		56.4	
(total)	P	10.5	7.9	9.2	13.7	10.4	5.8	6.5	6.3	11.9	10.6	14.2	10.7	3580		
	P/$\bar{B}$	0.26	0.20	0.21	0.24	0.13	0.14	0.11	0.12	0.16	0.14	0.19	0.28			63.5
Total	$\bar{B}$	242.1	234.7	277.6	390.3	440.7	275.9	278.6	296.6	313.9	514.5	477.1	251.5			
production	P	64.1	51.9	59.3	70.6	64.1	38.1	31.8	41.3	49.1	93.5	80.9	52.1	21 194.3	332.8	63.7
mean daily P/B ratio	P/$\bar{B}$	0.27	0.22	0.21	0.18	0.15	0.14	0.11	0.14	0.16	0.18	0.17	0.21			
Temperature in °C		29.3	28.4	28.8	28.5	25.6	22.2	20.8	21.8	24.5	27.0	27.6	29.9	mean annual temperature		26.2

Table 11 Mean daily production of the zooplankton (in mg m^{-3}) for each zone (A,B,...) and ratio $\Sigma P_j/\Sigma B$ calculated at a temperature of 22°C in the different regions of the lake sampled in February–March, 1971 (see text); N = nauplii; C = copepodids; A = adults.

	Southern open waters		Northern open waters and Archipelago				Southern Archipelago and reed islands				
	A (10)	B (10)	C (10)	D (10)	E (10)	F (10)	G (10)	H (9)	I (10)	J (5)	K (2)
M. micrura	4.5	1.4	2.4	0.7	0.2	1.5	7.6	1.2	18.5	17.8	9.2
D. excisum	2.0	1.1	1.8	0.1	0.2	1.5	4.4	3.9	16.5	15.1	6.7
B. longirostris	1.0	0.7	8.6	4.6	3.3	11.7	10.8	19.6	9.6	4.0	13.6
Daphnia	1.3	0.3	2.9	15.8	12.6	15.2	4.4	0.1	4.6	3.6	29.3
Ceriodaphnia	0.2	+	0	0	1.0	0	+	0	2.0	5.2	0
N. Cyclopoids	0.8	0.8	1.1	1.0	1.2	1.0	1.5	1.8	2.4	1.7	1.2
C. Cyclopoids	4.5	2.3	4.5	6.0	5.9	4.7	3.7	6.7	8.0	7.2	6.3
A. Cyclopoids	0.1	0.3	0.5	0.4	0.4	0.4	0.5	0.8	0.8	0.4	0.7
N. Calanoids	0.3	0.1	0.2	0.2	0.7	0.3	0.7	1.1	0.6	0.3	1.0
C. Calanoids	1.4	2.2	1.9	0.8	3.5	0.6	1.3	1.5	2.3	3.1	1.5
A. Calanoids	0.2	0.4	0.7	0.4	1.3	0.3	0.7	0.7	0.7	0.8	0.6
Cladocera	9.0	3.5	15.7	21.2	17.3	29.9	27.2	24.8	51.2	45.7	59.0
Cyclopoids	5.4	3.4	6.1	7.4	7.5	6.1	5.7	9.3	11.2	9.3	8.2
Calanoids	1.9	2.7	2.8	1.4	5.5	1.2	2.7	3.3	3.6	4.2	3.1
Total P (mg m^{-3})	16.3	9.6	24.6	30.0	30.3	37.2	35.6	37.4	66.0	59.2	70.3
$\Sigma P/\Sigma B$	0.18	0.10	0.13	0.16	0.11	0.17	0.15	0.14	0.18	0.19	0.18

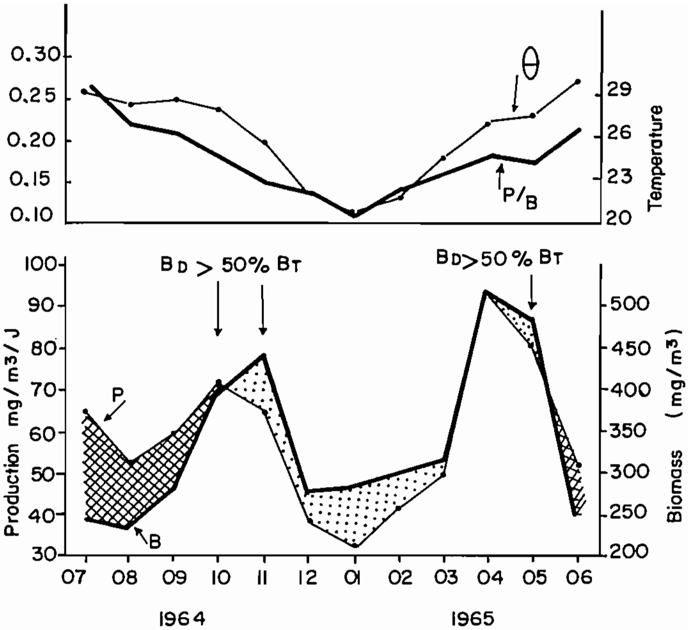

Fig. 7 Variations in the biomass (B), the production (P) and the production rate (P/B) of the planktonic microcrustaceans in the Eastern Archipelago during 1964–1965. B_D = biomass of the Calanoids; B_T = total biomass.

was 0.06 in 1964–1965 and ranged from 0.01 to 0.07 in 1972–1973. These variations are probably due to differences in the populations and the ecological conditions, but they also result from the different methods used.

12.1.2.3 *Between year variability.* Referring to the measurements of production made from 1968 to 1973, an increase in the production rate per unit D_e was observed in the Cladocera from 1968 to March 1973, especially in *Moina* at the Tchongolerom station. In the Calanoids, this rate was stabilized at about a mean value of 0.10. But it increased sharply in the Cyclopoids and Cladocera. In these three groups, there was a simultaneous increase in the fecundity of females (N_E/N_F) and probably a decrease in the duration of juvenile development leading to an increase in production rate, but also an increase in the proportion of adults that decreased this rate at least in the Copepods. The increase in fecundity and the acceleration in development observed in 1973 may have resulted from an improvement in nutritional conditions. As already shown, the consequences of these modifications varied with the populations: increase in the production rate of the Cladocera and Cyclopoids, stability of the Calanoids. It is interesting to note that the increase was greatest in species

(*Moina*, *Diaphanosoma* and Cyclopoids) where the increase in proportion of adult weight was lowest and that there was stability in the Calanoids where both the proportion of adults and this increase were highest.

A number of observations (Gras and Saint-Jean, in preparation) suggest that the previous variations represent a change, following the decrease in the water level preceding the drying up of the lake. This change was part of significant alterations in the composition of the populations and applied only to the region of the Eastern Archipelago. Between the periods of high and low waters the changes occurring in the composition were:

- a big decrease in the biomass of Cladocera that corresponded to the apparent disappearance of the genera *Daphnia* and *Bosmina*; while it was about 130 mg m^{-3} (37% of the total) at high water, it was only 40 mg (16.6%) during 1972–1973;
- during the 1972–1973 period, the substitution of *Tropodiaptomus* prevalent at high water by *Thermodiaptomus* which remained alone in March 1973 followed by the accelerated disappearance of this group just before the drying up. The Calanoids which represented 45% of the biomass on average during the period of high water represented only a quarter of it in March, 1973 and disappeared after the drying up period;
- an increase in the number of Cyclopoids, especially *Thermocyclops*.

The biomass of Cladocera was reduced by the biomass of the genera that disappeared: *Daphnia-Bosmina*. The remaining species, *Moina* and *Diaphanosoma*, approximately maintained their biomass but did not fill the gap left by the other genera. Therefore, at low water, only the most productive species remained and moreover, their production rate increased. The same phenomenon seemed to occur in the Copepods with a decrease in Calanoids and an increase in the number of *Thermocyclops*. On the whole, a relative stability in the production rate of the population was reached as already indicated.

With the above-mentioned changes in community composition, two states of production can be distinguished in this region of the lake. The first was during the period of high water up to 1972, when the Cladocera predominated forming 35 to 40% of the biomass and 2/3 of the production. The second corresponded to the low water when they contributed only about 40% of the production, that is to say a percentage similar to that of the Cyclopoids whose importance increased.

12.2 Benthos

12.2.1 *Biology of the main species and population structure*

The biology of some species and seasonal changes in their population structure must be studied before evaluating the production of the natural populations through classical methods. Observations on the benthic fauna of Lake Chad have referred mainly to the molluscs (Lévêque 1973a), although some data about Chironomids (Dejoux 1976) and Oligochaetes (Dejoux et al. 1969) are also available.

12.2.1.1 *Molluscs.* Quantitative samples were taken over a year from different biotopes of three sites on the lake (Bol, Samia, Baga Kawa) as well as in the delta of the Shari. The size structure of the populations of the main species was determined each time a sample was taken and the dimensions considered were height of shell for Prosobranchia and its length for Lamellibranchia. From the analysis of these demographic measurements some data were obtained on the biology of the species. They were supported by observations from *in situ* cultures in boxes containing previously sifted sediment, covered with a mosquito net and immersed on the bottom. Individuals of a known size were put into these cultures and measured at more or less regular intervals (Lévêque 1971).

Corbicula africana has a seasonal reproductive cycle that was shown by the analysis of its size structure at various stations (Lévêque 1973). However, the juveniles in the population occurred at the beginning (Bol) or the end of the cool season (Samia, Shari delta) according to the sites, and the reproductive season lasted several months. The life-span in culture seemed to range from 1 to 2 years under the usual lacustrine conditions, but it could be longer in certain particular environments. It was thus possible to follow the growth of a cohort in the Shari delta from December, 1967 when it was one year old, up to 1969 when it was three years, with the biggest individuals reaching 20 mm. In 1965, some larger *Corbicula* were collected in a drying backwater situated close to the Shari delta. The factors limiting the life span and growth of *Corbicula* in the lake are not known.

Bellamya unicolor is a viviparous and dioecious species whose juveniles in the distal end of the uterus at birth are about 3 mm. Some biological aspects of this species were studied with *in situ* cultures. It was thus possible to follow growth and specify the age at first reproduction (Fig. 8) which was about two and a half months in the warm season (28–30°C) and three and a half months in the cool season (20°C). The survival curves (Fig. 9) showed that the maximum life span was 15 months, 50% of the individuals disappearing between 5 and 7 months. Reproduction was continuous, but fecundity followed a seasonal cycle with a maximum in the warm season and a minimum in the cool season. The number of births in culture expressed monthly for each adult individual (mixed sexes) ranged from 7 to 1.5 (Fig. 10). In the size structure of the natural populations, both an adult and a juvenile pattern could be observed, clearly distinct throughout the year, suggesting a high death rate in the latter, since recruitment was continuous.

Though little is known about *Cleopatra bulimoides* the demographic struc-

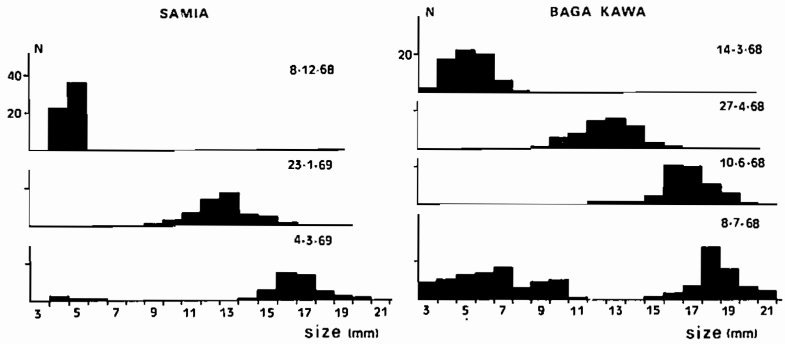

Fig. 8 ***Bellamya unicolor*****: changes in size structure of *in situ* cultures showing the growth and occurrence of the first births (Lévêque 1973).**

tures showed that reproduction could occur throughout the year with maximum values during periods that varied according to the stations. Since the adult size was reached three or four months after birth in culture it can be assumed by comparison with *B. unicolor* that first reproduction occurs about 3 months after birth. The maximum life-span appeared to range from 1 to 2 years and the largest sizes observed were 14–15 mm.

Melania tuberculata is considered ovoviviparous and parthenogenetic (Morrison 1954). According to its demographic structure, reproduction occurred throughout the year; however, with a major decrease in the cool season. In cultures first reproduction occur about two and a half months after birth and the size ranged from 9 to 10 mm. Under the general conditions of Lake Chad, maximum size ranged from 17 to 18 mm, but, as in the case of *Corbicula*, growth exceeded this limit under certain conditions and individuals from 20 to 30 mm were collected in a few shallow places in the lake.

When analyzing demographic structures, it can be pointed out that the young Prosobranchia, with a few exceptions, were generally not very numerous in relation to adults in the natural populations, although their reproduction was continuous. This anomaly can be accounted for only by considerable mortality after birth resulting partly from the predation exerted by fishes. Lauzanne (1975) compared the size of the molluscs caught in the natural environment with those of the molluscs contained in the stomachs of three malacophagous fishes in the Eastern Open Water: *Synodontis schall*, *Synodontis clarias*, *Hyperopisus bebe*. It appears (Fig. 10) that the three species of fish behaved similarly and their predation was exerted mainly on young individuals. However, the phenomenon was a little less clear in *Corbicula* whose young were consumed less than the young Prosobranchia.

In the Eastern Open Water where these malacophagous fishes represented about 7% of the total weight of the catches in gill nets in 1970, the predation on

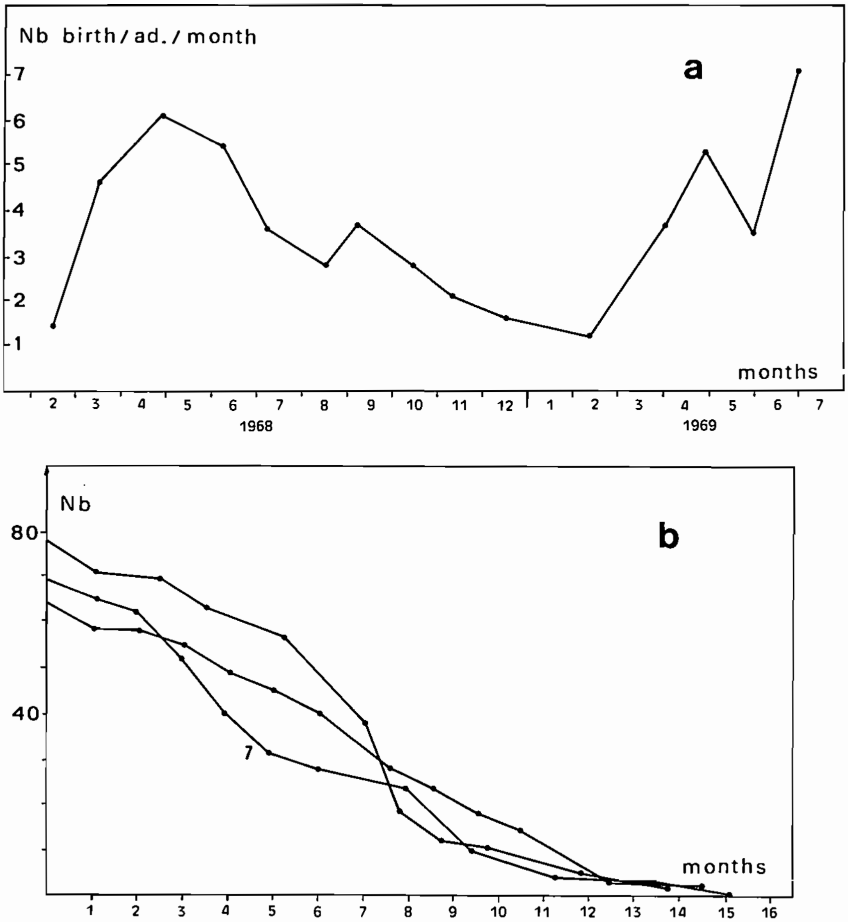

Fig. 9 ***Bellamya unicolor*** **in** ***in situ*** **cultures at Bol; (a) monthly number of births for each adult individual over the year; (b) survival curves for three cohorts (Lévêque 1973).**

young molluscs must have been important quantitatively and played a prime role in the dynamics of the snail populations. Of course, this phenomenon occurred in the whole lake and it accounts for the small proportion of young molluscs in the populations. In fact, Lauzanne (1975) considered that *S. schall* consumed about two hundred molluscs a day and *S. clarias* about one hundred.

It was often difficult to evaluate the growth of the molluscs only by studying their size structures, especially as reproduction was continuous or at least staggered in time. Therefore, we referred to the *in situ* cultures to determine the growth curves and the parameters of von Bertalanffy's equation were calculated through the method of instantaneous increments from the results thus obtained (Table 12).

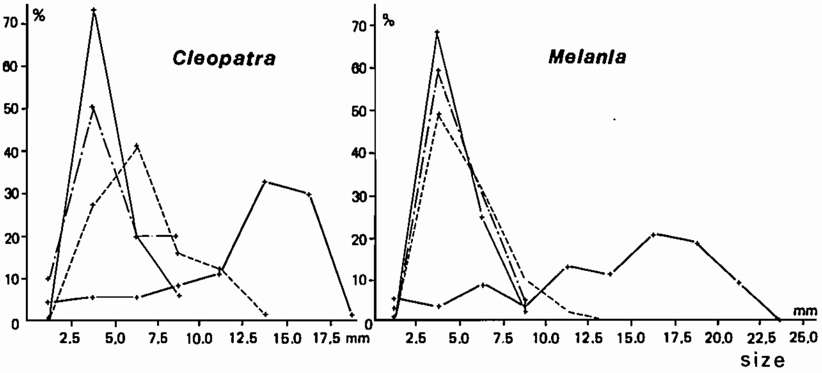

Fig. 10 Distribution of the size classes for two species of benthic molluscs consumed by fishes. The benthic population is represented by thick lines, the individuals present in the stomachs of *Synodontis clarias* by thin lines, *Synodontis schall* by dashed lines and *Hyperopisus bebe* by dashed and dotted lines.

Table 12 Growth of the benthic molluscs in Lake Chad: values of the parameters K and L∞ from Von Bertalanffy's equation for the main species at various stations.

	K	L∞ (mm)
Corbicula africana		
— Bol	0.221	10.0
— Baga Kawa	0.115	14.2
— Shari delta	0.127	13.9
Caelatura aegyptiaca		
— Bol	0.152	26.8
— Baga Kawa	0.114	33.8
Caelatura teretiuscula		
— Bol	0.159	28.1
Mutela rostrata		
— Bol	0.179	59.3
Mutela dubia	0.129	76.4
Cleopatra bulimoides		
— Baga Kawa	0.920	11.6
— Samia	0.624	12.1
Melania tuberculata		
— Baga Kawa	0.307	15.9
Bellamya unicolor		
— Bol	0.969	19.5

The influence of local ecological conditions on the growth rate and the resulting maximum sizes, can be seen by comparing the growth curves of the same species from various stations. In particular, this was true for *Caelatura aegyptiaca* which grew more rapidly at Baga Kawa than at Bol. On the other hand, many species grew less rapidly in the cool season probably because of the drop in temperature which was rather marked at that time.

The size–weight relationships calculated for the dry organic weight (without shell), the weight of the shells and the fresh weight including the shell (Lévêque 1973) were used to determine the growth curves for weight and to calculate the increase in weight for the four main species over 15 days. There were two distinct groups:

- *Bellamya* and *Cleopatra* grew very quickly during the first months, after which first reproduction occurred. Growth was then reduced and the maximum size of the oldest individuals was only slightly above that at first reproduction. This maximum size varied a little according to the sites and the ecological conditions, but the growth rate remained the same. In fact, these species have a maximum life span which did not seem to exceed one and a half years.
- In contrast, in *Melania* and *Corbicula*, first reproduction and the death of the individuals occurred before the animal reached its potential maximum size. This explains the absence of an asymptote in the growth curve of *Corbicula*, since it was determined only for a life-span of one and a half year while the species can live and grow for a much longer time. The same held true for *Melania* as shown previously.

There were, therefore, basic differences in production between the two groups. The production resulting from the increase in weight of the *Bellamya-Cleopatra* group was very high in the young individuals and less important in the adults, while in the *Melania-Corbicula* group, production from growth occurred throughout the entire life of the individuals at least when the latter were of the size commonly found in the lake.

12.2.1.2 *Oligochaeta and insects*. The duration of the larval stage (from egg to adult) was determined for two Chironomids. It was 17 days at 26°C and 13 days at 30°C in the laboratory for *Chironomus pulcher* (Dejoux, 1971) and 18 days between 18 and 23°C for *Tanytarsus nigrocinctus* (Fig. 11) under almost natural conditions (Dejoux 1976).

An attempt was made to evaluate the duration of larval growth for a few species of Chironomids based on the rhythm of emergence during a lunar cycle in the cool season in January 1973 (Dejoux 1976). It seems that the majority of these species have a larval stage with a duration of 15 days or a little less. However, these results should be checked in culture.

Oligochaetes reproduce throughout the year, but reached a maximum in the cool season (Dejoux et al. 1969). This group was not studied in detail.

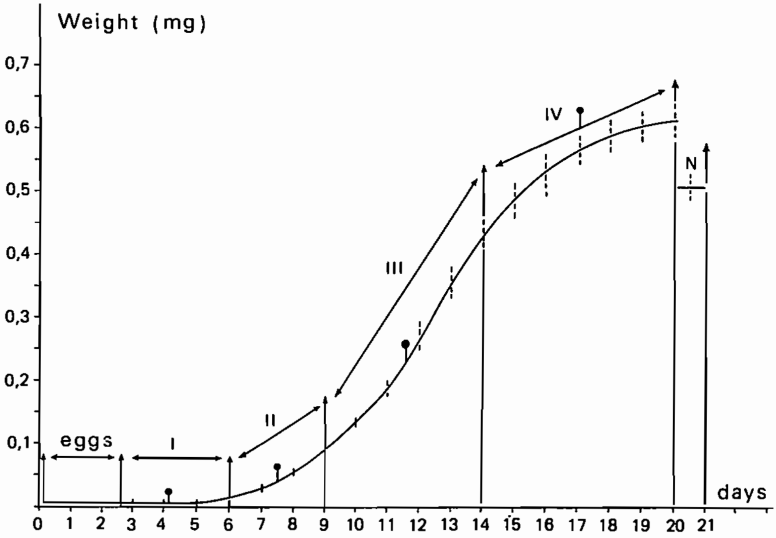

Fig. 11 Growth curve in weight and growth stages of *T. nigrocinctus*.

12.2.2 *Production*

Among the three groups of benthic organisms investigated, the molluscs are the only ones to have been thoroughly studied (Lévêque 1973a). Production was evaluated in various biotopes at three sites situated in different regions of the lake. Here *in situ* cultures and regular sampling allowed the study of growth rates and changes in demographic structures of the populations of the main species.

Since reproduction is continuous or at least evenly distributed in time, it was not possible to distinguish cohorts and to use simple methods of calculating production. Therefore, a method was developed (Lévêque 1973a) based on the evaluation of an instantaneous growth rate of the population (G) at the time of each sample.

The annual $P/\bar{B}$ ratio was calculated for the populations of each species (Table 13) to be able to apply the results thus obtained to the whole lake and to draw a parallel between the different stations. The $P/\bar{B}$ values varied for the same species according to the stations. However, they were maintained within rather narrow limits. The highest $P/\bar{B}$ values were found for *Bellamya* and *Melania* which were the predominant species in the whole lake (Lévêque 1972) according to biomass and numbers.

From a knowledge of the life-span of the species, the results obtained can be compared to the theoretical values of $P/\bar{B}$, determined in relation to the life-span for populations in equilibrium (Lévêque et al. 1977). The observed values

Table 13 Mean biomasses (in g m^{-2}) and annual $P/\bar{B}$ ratios for the main species in the stations under study.

Species	Station	Organic matter production		Shell production	
		$\bar{B}$ in g	$P/\bar{B}$ annual	$\bar{B}$ in g	$P/\bar{B}$ annual
Melania tuberculata	Samia 1	3.5	4.4	28.5	5.0
	Samia 2	0.7	3.0	5.6	3.1
	Baga Kawa 1	0.9	5.3	6.8	5.7
	Baga gawa 3	1.5	4.8	12.3	5.2
Cleopatra bulimoides	Samia 1	3.6	2.0	27.5	2.3
	Samia 2	3.6	1.7	28.0	2.1
	Baga Kawa 1	3.6	2.5	26.3	3.0
	Baga Kawa 3	3.4	3.5	25.5	3.6
	Bol 2 1968	0.8	2.4	5.8	2.8
	1969	0.5	2.8	3.6	3.4
	Bol 3 1968	0.3	2.5	2.2	2.9
	1969	1.8	3.5	13.7	4.1
Bellamya unicolor	Baga Kawa 2	2.8	5.5	18.0	6.0
	Baga Kawa 3	2.1	6.1	13.4	6.5
Corbicula africana	Samia 1	1.1	2.8	34.8	3.0
	Samia 2	0.5	2.4	16.1	2.6
	Baga Kawa 1	1.7	2.3	56.6	2.6
	Baga Kawa 2	3.7	2.9	121.4	3.0
	Baga Kawa 3	1.3	2.1	43.1	2.2
	Bol 3	1.3	2.8	46.3	3.1

of $P/\bar{B}$ for *Bellamya* (life-span: 1 year; $P/\bar{B}=5.8$) and *Melania* (1.5 years; $P/\bar{B}=4.4$) are close to the theoretic values. The same was true for *Corbicula* ($P/\bar{B}=2.6$) if it is estimated that this last species can reach an average of 2 years. On the other hand, the value observed for *Cleopatra* ($P/\bar{B}=2.6$) is much lower than the theoretical value expected for a life-span ranging from 1 to 1.5 years. This phenomenon could have been caused by a variety of factors including a miscalculation of the life-span, death rate or growth. However, we also noted that the young stages were rather rare in the populations of this species, while the adults, whose production was low, prevailed. This finding is comparable to the observations on the populations of the lake where a decrease was noted from 1968 to 1970 in the density of *Cleopatra* which was replaced by *Melania* in several biotopes in the south basin. Therefore, the population would no longer be in equilibrium and would decline, explaining the rather low P/B̄ values of *Cleopatra*.

When calculating production, we could also show that a rather strong relation existed between the instantaneous growth rate of the population (G), which corresponded to a daily P/B̄, and the average weight of individuals (W̄) (Fig. 12). Such empirical relationships are interesting from a practical point of view insofar as they make it possible to quickly calculate production of sampled populations from the mean weight of the individuals (Lévêque 1973a).

From knowledge of the molluscan stocks in Lake Chad in 1970 and the P/B̄ ratio for the main species, we estimated the annual production of molluscs in Lake Chad (Table 14). It was 279 000 tons of organic matter (dry weight) and 1 883 000 tons for the shells, that is an average of 14.5 g/m^2/year and 98 g/m^2/year respectively. If the caloric equivalents are used (Table 15), then

Table 14 Mean P/B̄ ratios calculated for the main species of benthic molluscs in Lake Chad and evaluation of the annual production for the whole lake in 1970. The values are expressed in tons (dry weight).

Species	Organic matter		Shell	
	P/B̄	P	P/B̄	P
Melania	4.4	60 852	4.8	513 000
Bellamya	5.8	162 122	6.2	996 500
Cleopatra	2.6	44 996	3	183 200
Corbicula	2.6	4711	2.8	124 000
Caelatura	2.0	6410	2.2	9300
Total		279 091		1 883 500

Table 15 Evaluation of the annual production of benthic molluscs in the various zones of Lake Chad in 1970 (Fig. 11, Chapter 8).

Zones	Area (km^2)	P (g m^{-2} yr^{-1})	P (Kcal m^{-2} yr^{-1})
1	3082	0.1	0.4
2	3871	35.3	141
3	1501	24.1	96
4	2133	25.6	102
5	2290	11.4	46
6	2083	3.8	15
7	4259	3.0	12

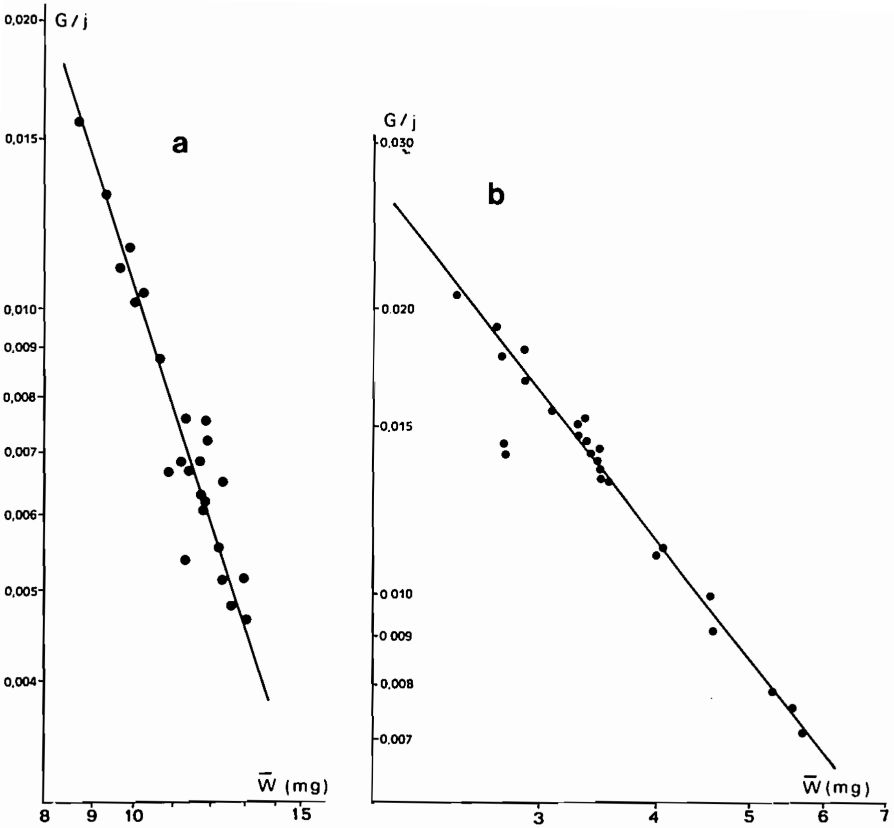

Fig. 12 Relationships between the instantaneous growth rate of the populations (G) and the mean weight of an individual belonging to these populations (W̄) expressed in mg of the dry body weight; (a) *Cleopatra bulimoides*; (b) *Melania tuberculata* (from Lévêque 1973).

the total production of organic matter was 1116 × 10^9 Kcal, that is an average of 58 Kcal/m^2/year.

Most of the production resulted from the three species of Prosobranchia (Table 14) among which *Bellamya* played the most important role. In other respects, the distribution of this production was irregular in the lake (Table 14), since the zones with the highest production were those which had the highest biomasses such as the Northeastern Archipelago, the Northern Open Water and the Great Barrier.

It is obvious that the above-mentioned estimates are valid only for the year 1970 and they can undergo profound modifications according to the lake level and its water area. However, these observations can be applied to the period of 'Normal Chad' since the biomass estimates made in 1968 were similar to those for the year 1970. The production of shells was considerable and required about

700 000 tons of calcium as the shells contain 37% calcium in the form of aragonite. This was four times the annual mean supply of calcium to the lake or half the dissolved lacustrine stock of this element (Carmouze 1976). Therefore, the molluscs play a significant role in the regulation of calcium in Lake Chad.

Observations on the production of *T. nigrocinctus* (Chironomidae) showed that the average daily $P/\bar{B}$ ratio was 0.24 in the cool season at a station situated in the north basin (Dejoux 1976). However, this result cannot be applied to the total biomass of the benthic insects of which Chironomidae represent only a part.

12.2.3 *Energy balance*

Energy ingested as food can be utilized in different ways: part of it is used to make organic matter, production (P); another part is used for metabolic processes and can be measured by oxygen consumption, respiration (R); finally, a part of it is excreted without being digested (F) and as excretory products (U). The equation, $C=P+R+F+U$, expressed in comparable energy bits (the calorie) represents an energy budget (Klekowski 1970). Assimilation is also defined by $A=P+R$.

For the benthic molluscs of Lake Chad we only determined the assimilation budget, because the evaluation of excretion raised problems that were impossible to solve with the means available.

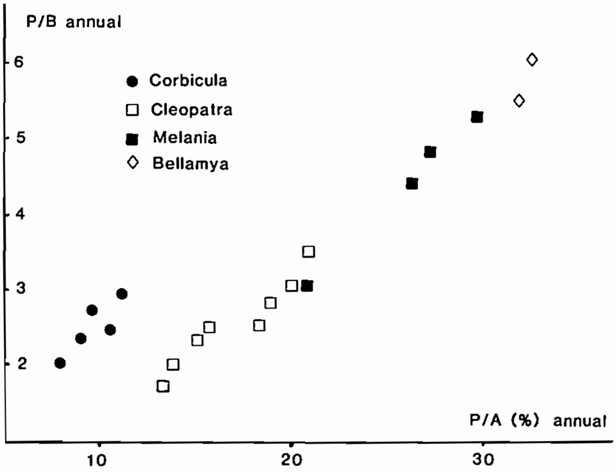

Fig. 13 Relationships between the annual P/B and the annual P/A foţ the natural populations of the various species of benthic molluscs in Lake Chad. Each point corresponds to a population of the species under studies.

Table 16 Measurement of oxygen consumption of the benthic molluscs; values of the constants a and b for the relation $R = aW^b$ and correlation coefficient (r) of the straight line between log R and log W. R is expressed in terms of microliter/individual/hour and W in terms of mg of dry organic weight (D.O.W.) or fresh weight including the shell (F.W.).

Species	Locality	Temp. °C	Date	Number of replicates	Size range (mm)	R=f(D.O.W.)			R=f(F.W.)		
						a	b	r	a	b	r
Cleopatra bulimoides	Baga Kawa	21.5	26/1/70	25	7 à 12	1.97	0.768	0.884	1.02	0.531	0.884
	Baga Kawa	29.5	22/10/69	46	8 à 13	2.51	0.790	0.921	1.40	0.527	0.918
Melania tuberculata	Samia	29	25/10/69	38	5 à 13	1.60	0.930	0.980	0.24	0.788	0.980
	Samia	29	26/10/69	41	5 à 14	1.59	0.909	0.987	0.23	0.793	0.986
	Samia	20.5	23/1/70	32	7 à 14	1.25	0.747	0.976	0.22	0.684	0.976
Bellamya unicolor	Baga Kawa	20.5	26/1/70	43	9 à 18	2.39	0.829	0.974	0.44	0.743	0.974
	Baga Kawa	30	19/10/69	45	6 à 17	2.56	0.905	0.979	0.40	0.811	0.979
	Bol	20.5	20/1/70	30	8 à 19	3.16	0.702	0.984	0.46	0.710	0.983
	Bol	32	20/8/69	27	8 à 19	7.30	0.666	0.991	1.18	0.671	0.991
	Bol	26	23/8/69	66	5 à 17	2.17	0.790	0.975	0.32	0.797	0.975
Corbicula africuna	Delta	29.5	28/10/69	43	4 à 13	7.36	0.638	0.997	0.86	0.578	0.991

Table 17 Calorific values for the tissues of the five main species of benthic mollusc in Lake Chad (Lévêque 1973).

Species	Locality	Number of replicates	Calorific value in cal g^{-1} dry weight	% ash	Calorific value in in cal g^{-1} without ash
Bellamya unicolor	Samia	5	4141±65	15.7±1.4	4919±95
Bellamya unicolor	Baga Kawa	3	3982±197	16.7±1.5	4777±319
Cleopatra bulimoides	Samia	3	3989±140	15.4±1	4730±127
Melania tuberculata	Samia	3	3818±232	17.7±3.4	4636±88
Melania tuberculata	Baga Kawa	1	3678	22.6	4751
Corbicula africana	delta du Chari	3	4974±25	12.8±1.6	5707±83
Caelatura aegyptiaca	Baga Kawa	5	3972±149	19.7±2	4949±164

Respiration was measured experimentally in the field during different seasons (Lévêque 1973b) by using individuals which had just been collected and whose physiological condition was *a priori* closer to the natural conditions than those of the individuals maintained in culture. The relationships between the amount of oxygen consumed (in µl/ind/h) and the weight of individuals expressed in fresh weight including the shell (F.W.) or in the dry weight of the organic matter (D.O.W.) were calculated for different size ranges and at different temperatures (Table 16).

The oxycalorific coefficient of 4.86 cal/ml of oxygen (Winberg 1971) was used to convert the volume of oxygen consumed into calories. These results, as well as the measurements of production were used to determine assimilation for the different populations of the main species and to calculate the utilization

Table 18 Production, respiration and assimilation (in Kcal m^{-2} $year^{-1}$), annual P/B̄ ratio and P/A (%) for the different populations of benthic mollusc that were studied in Lake Chad.

	R (Kcal m^{-2} yr^{-1})	P (Kcal m^{-2} yr^{-1})	A (Kcal m^{-2} yr^{-1})	P/A (%)	P/B annual
Bellamya unicolor					
Baga Kawa station 2	120.9	58.4	179.3	32.5	5.5
Baga Kawa station 3	116.9	55.0	171.9	32.0	6.1
Cleopatra bulimoides					
Samia station 1	183.8	29.2	213.0	13.7	2.0
Samia station 2	163.9	25.6	189.5	13.3	1.7
Baga Kawa station 1	164.1	36.8	200.9	18.3	2.5
Baga Kawa station 3	187.7	49.3	237.0	20.8	3.5
Bol station 3 1968	13.6	2.5	16.1	15.6	2.5
Bol station 3 1969	90.2	23.0	113.2	20.3	3.5
Bol station 2 1968	43.3	7.8	51.1	15.2	2.4
Bol station 2 1969	24.7	5.8	30.5	19.0	2.8
Melania tuberculata					
Samia station 1	172.7	61.8	234.5	26.4	4.4
Samia station 2	30.8	7.9	38.7	20.5	3.0
Baga Kawa station 1	43.4	18.4	61.8	29.8	5.3
Baga Kawa station 3	34.0	12.8	46.8	27.3	4.8
Corbicula africana					
Samia station 1	145.1	16.9	162.0	9.7	2.8
Samia station 2	60.0	6.3	66.3	8.9	2.4
Baga Kawa station 1	202.3	21.3	227.4	11.1	2.3
Baga Kawa station 2	446.7	51.9	498.6	10.4	2.9
Baga Kawa station 3	116.4	11.5	127.9	9.0	2.1

efficiency of energy assimilated for growth (P/A) (Table 18). It seems that there was a rather linear relation between the annual $P/\bar{B}$ and P/A for the three species of Prosobranchia (Fig. 13). On the contrary, for P/B ratios that were identical in size the P/A ratio was much lower in *Corbicula*. This difference could be accounted for by the fact that the ratio of dry body weight to the shell weight ranged from 1/7 to 1/9 in Prosobranchia, while it was four times lower in *Corbicula* (1/35). Therefore, it would be necessary for this last species to use a greater amount of energy per unit of dry weight than Prosobranchia, in order to form its shell. The P/A values observed in the molluscs of Lake Chad were consistent with most previous results which had already been obtained with other mollusc species (Lévêque 1973b).

References

Burgis, M. J., 1971. The ecology and production of copepods, particularly *Thermocyclops hyalinus*, in the tropical Lake George, Uganda. Freshwat. Biol. 1: 169–192.

Carmouze, J. P., 1976. La régulation hydrogéochimique du lac Tchad. Trav. Doc. ORSTOM, No. 58, 418 pp.

Dejoux, C., 1971. Recherches sur le cycle de développement de *Chironomus pulcher*. Can. Ent. 103: 465–470.

Dejoux, C., 1976. Synécologie des Chironomides du lac Tchad (Diptères, Nématocères). Trav. et Doc. ORSTOM, No. 56, 161 pp.

Dejoux, C., Lauzanne, L. and Lévêque, C., 1969. Evolution qualitative et quantitative de la faune benthique dans la partie est du lac Tchad. Cah. ORSTOM Sér. Hydrobiol. 3: 3–58.

Ferguson, A. J. D., 1975. Invertebrate production in lake Turkana (Rudolf)-Symposium on the Hydrobiology and fisheries of Lake Turkana, 25–29th May, 1975, 28 pp., mimeo.

Gras, R., 1970. Poids individuel, durée de développement et production des différents stades de *Tropodiaptomus incognitus* (Crustacés, Copépodes). Cah. ORSTOM Sér. Hydrobiol. 4: 63–70.

Gras, R. and Saint-Jean, L., 1969. Biologie des crustacés du lac Tchad. 1. Durée de développement embryonnaire et post-embryonnaire: premiers résultats. Cah. ORSTOM Sér. Hydrobiol. 3: 43–60.

Gras, R. and Saint-Jean, L., 1976. Durée du développement embryonnaire chez quelques espèces de Cladocères et de Copépodes du lac Tchad. Cah. ORSTOM Sér. Hydrobiol. 10: 233–254.

Gras, R. and Saint-Jean, L., 1978a. Taux de natalité et relations entre les paramètres d'accroissement et d'abondance d'une population de Cladocères à reproduction par parthénogenèse. Cah. ORSTOM. Sér. Hydrobiol. 12: 19–63.

Gras, R. and Saint-Jean, L., 1978b. Durée et caractéristiques du développement juvénile de quelques Cladocères du lac Tchad. Cah. ORSTOM Sér. Hydrobiol. 12: 119–136.

Gras, R. and Saint-Jean, L., 1981a. Durée de développement juvénile de quelques copépodes planctoniques du lac Tchad. Rev. Hydrobiol. trop. 14: 39–51.

Gras, R. and Saint-Jean, L., 1981b. Croissance en poids de quelques Copépodes planctoniques du lac Tchad. Rev. Hydrobiol. trop. 14: 135–147.

Klekowski, R. Z., 1970. Bioenergetic budgets and their application for estimation of production efficiency. Pol. Arch. Hydrobiol. 17: 55–80.

Lauzanne, L., 1975. La sélection des proies chez trois poissons malacophages du lac Tchad. Cah. ORSTOM Sér. Hydrobiol. 9: 3–7.

Lévêque, C., 1971. Equation de von Bertalanffy et croissance des mollusques benthiques du lac Tchad. Cah. ORSTOM Sér. Hydrobiol. 5: 263–283.

Lévêque, C., 1972. Mollusques benthiques du lac Tchad: écologie, étude des peuplements et estimation des biomasses. Cah. ORSTOM Sér. Hydrobiol. 6(1): 3–45.

Lévêque, C., 1973. Dynamique des peuplements, biologie et estimation de la production des mollusques benthiques du lac Tchad. Cah. ORSTOM Sér. Hydrobiol. 7: 117–147.

Lévêque, C., Durand, J. R. and Ecoutin, J. M., 1977. Relations entre le rapport P/$\bar{B}$ et la longévité des organismes. Cah. ORSTOM Sér. Hydrobiol. 11: 17–32.

Morrisson, J. P. E., 1954. The relationships of Old and New World Melanians. Proc. U.S. nat. Mus. 103: 357–394.

Winberg, G. G., 1971. Methods for the estimation of production of Aquatic animals. Academic Press, London and New York, 175 pp.

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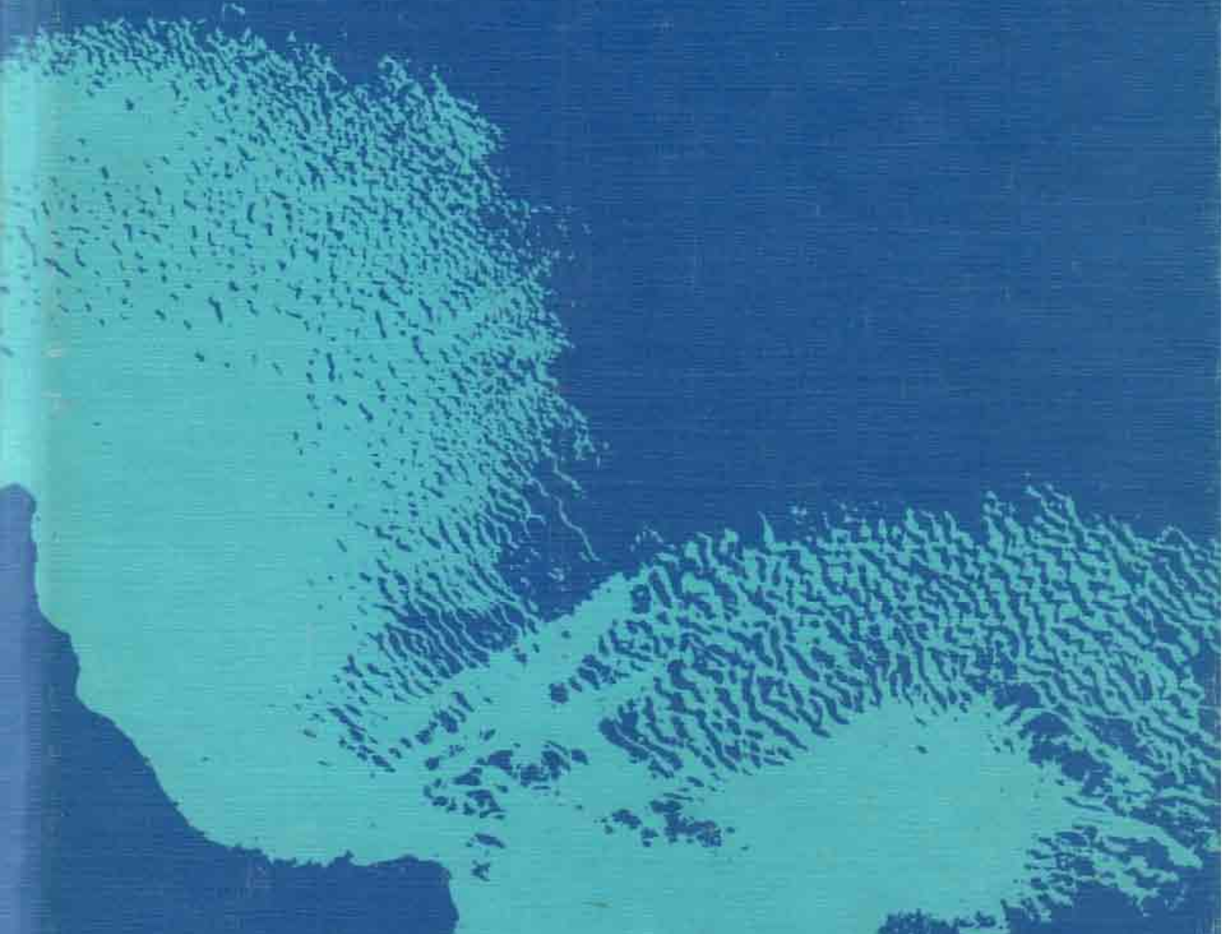

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