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Population growth capacities and regulatory factors in monospecific cultures of the cladocerans *Moina micrura* and *Diaphanosoma excisum* and the copepod *Thermocyclops decipiens* from Côte d'Ivoire (West Africa)

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Abstract − The cladocerans *Moina micrura* and *Diaphanosoma excisum* and the copepod *Thermocyclops decipiens* were studied in microcosms (0.8 m^3) under semi-controlled experimental conditions at 25–29 °C for 32 days, by daily sampling after an initial monospecific inoculation. For each species, the time series began with an exponential population growth phase. *M. micrura* showed a higher daily population growth rate (mean = 1.19) than *D. excisum* (0.78) and *T. decipiens* (0.45). The growth phase of *M. micrura* coincided with bacterial and phytoplanktonic peaks while the growth phase of the two other species followed these peaks. After this phase, *M. micrura* quickly disappeared (day 10), while *D. excisum* biomass decreased but showed a second increase, followed by a stabilization sequence. *T. decipiens* biomass had a slower increase and stabilized after day 17. The passage to sexual reproduction in relation to crowding was the main regulating factor for *M. micrura*, whereas food limitation was important for *D. excisum*. For *T. decipiens*, population growth was limited by decreased recruitment to copepodite stages which could have resulted from cannibalism exerted by older stages. © 2000 Ifremer/Cnrs/Inra/Ird/Cemagref/Éditions scientifiques et médicales Elsevier SAS

zooplankton / population growth rates / microcosms / *Moina micrura* / *Diaphanosoma excisum* / *Thermocyclops decipiens* / Côte d'Ivoire

Résumé − Capacités de croissance et facteurs de régulation en cultures monospécifiques chez les cladocères *Moina micrura* et *Diaphanosoma excisum* et le copépode *Thermocyclops decipiens* de Côte d'Ivoire (Afrique de l'Ouest). Les cladocères *Moina micrura* et *Diaphanosoma excisum* et le copépode *Thermocyclops decipiens* ont été étudiés au cours de séries temporelles de 32 jours en microcosmes à une température de 25–29 °C, à partir d'un ensemencement initial monospécifique. Pour chaque espèce, on observe une phase d'accroissement exponentielle avec un taux d'accroissement journalier beaucoup plus élevé chez *M. micrura* (moyenne de 1,19) que chez *D. excisum* (0,78) et *Thermocyclops* (0,45). Chez *M. micrura*, la phase d'accroissement coïncide avec les pics bactérien et phytoplanctonique alors que chez les deux autres espèces elle est postérieure à ces pics. Après cette phase, *M. micrura*, disparaît rapidement (10^e jour), *D. excisum* décroît mais présente ensuite un 2^e développement suivi d'une période de stabilisation et enfin *Thermocyclops* continue à augmenter plus lentement et se stabilise après le 17^e jour. Le passage à un mode de reproduction sexué lié à la sur-densité est le processus de régulation dominant chez *M. micrura* alors que la régulation trophique semble déterminante chez *D. excisum*. Chez *Thermocyclops*, un fort ralentissement, voire un arrêt, du recrutement des stades copépodites, semble être déterminant et pourrait résulter du cannibalisme exercé par les stades les plus âgés. © 2000 Ifremer/Cnrs/Inra/Ird/Cemagref/Éditions scientifiques et médicales Elsevier SAS

zooplancton / taux d'accroissement de la population / microcosmes / *Moina micrura* / *Diaphanosoma excisum* / *Thermocyclops decipiens* / Côte d'Ivoire

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1. INTRODUCTION

Because fish and crustaceans constitute major supplies of animal protein in developing countries, aquaculture and inland fisheries have shown a considerable development in the tropical zone over the last two decades (Petr, 1994). In aquaculture, an increasing demand exists for live zooplankton of suitable size and quality to serve as prey for crustaceans and fish larvae. Common prey are *Artemia* (Versichele et al., 1986) and rotifer species (Pourriot, 1986), but there is a growing interest for cladoceran (Adeyemo et al., 1994; Ganzon-Naret and Ferming, 1994) and copepods (Stottrup and Norsker, 1997). Preys can be collected from natural planktonic communities (Barnabé, 1986) or raised in fertilized monospecific cultures (De Pawn et al., 1981; Bonou and Saint-Jean, 1998). Production of zooplankton in rearing ponds may be useful in aquaculture (Geiger, 1983), but this approach needs to control microbial activity in relation to nutrient flow (Costa-Pierce and Craven, 1987). Zooplankton cultivation as well as management of natural or semi-natural systems to produce animal food require information on the ecological characteristics of the studied species.

The cladocerans *Moina micrura* and *Diaphanosoma excisum* and the copepod *Thermocyclops decipiens* are common species in West African lentic waters. In Côte d'Ivoire, they are often major components of lakes and reservoirs (Yté et al., 1996; Aka et al., 2000) and they have been used as food for larvae of the catfish *Heterobranchus longifilis* (Hem et al., 1994). Many studies have shown that *Moina* (Khandal and Rajbanshi, 1995; Alam et al., 1995) and *Diaphanosoma* (Sripayatt, 1981; de la Pena et al., 1998) species have promising characteristics for aquaculture but much less is known on *Thermocyclops* (Mavuti, 1994).

Preceding studies in Côte d'Ivoire have shown the high growth capacities of *M. micrura* and *D. excisum*, in various conditions: fertilized aquaculture ponds (Saint-Jean and Bonou, 1994), outdoor mesocosms (Bonou and Saint-Jean, 1998) or laboratory experiments (Bonou et al., 1991). Previous works on cyclopoid copepods have shown the promising potential of *Mesocyclops leuckarti* in laboratory conditions (Bonou et al., 1991) and of *Apocyclops panamensis* in a brackish water pond (Pagano et al., 1999). No equivalent study was made for *Thermocyclops* species, but the high biomass they sometimes reach in natural conditions [up to 1 000 µg $C{\cdot}L^{-1}$ from Aka et al. (2000)] should indicate that they have high potential for production in controlled systems.

In this study, our objectives were to analyse and compare the growth capacities of *Moina micrura*, *Diaphanosoma excisum* and *Thermocyclops decipiens* in monospecific cultures and to analyse the factors that regulate population growth in the absence of competition and predation.

2. MATERIALS AND METHODS

Moina micrura, *Diaphanosoma excisum* and *Thermocyclops decipiens* were raised for 32 days in six (3 × duplicates) cylindrical resin tanks (1.6 m in diameter, 0.5 m in height and 0.4 m in water height) under a transparent porch-roof at the CRO laboratory in Abidjan.

2.1. Tank manipulation

Each tank was filled on 8 May 1994 with 0.8 m^3 tap water and immediately fertilized with 55 mg chicken manure. Afterwards, 30 mg of chicken manure were poured into each tank every 2 days until d9 and every 3 days afterwards to insure a good level of fertilization (Bonou and Saint-Jean, 1998). Before each fertilization, the manure was mixed with 0.5 L of water and sieved through a net of 60 µm mesh size to remove large aggregates.

On 9 May (d0), all tanks were inoculated with the same quantity of phytoplankton mixture at an initial chlorophyll concentration of approximately 3 $\mu g{\cdot}L^{-1}$. The algal mixture had been prepared a few days before using natural assemblages from nearby aquaculture tanks in order to cover a wide range of algal size (*table I*). The tanks, named using the first letter of the zooplankton genus inoculated (M1, M2; D1, D2; T1, T2), were permanently covered with mosquito nets to avoid insect breeding. Their water level was maintained daily by adding new tap water to compensate for evaporation.

Inoculation with zooplankton was performed 2 days after phytoplankton (d2) with populations previously reared in 20-L buckets that had two mesh-covered windows (8 cm in diameter, 240 µm mesh size) and were immersed in eutrophic tanks. Two equivalent sets of inocula (mainly adults and older developing stages) were prepared for each species and gently poured into duplicate tanks. Inoculation densities were 9 $ind.{\cdot}L^{-1}$ for *M. micrura*, 10 $ind.{\cdot}L^{-1}$ for *D. excisum* and 3 $ind.{\cdot}L^{-1}$ for *T. decipiens*.

2.2. Environmental variables

Water temperature and dissolved oxygen were recorded, at mid depth, continuously in two tanks (D1 and T1) with a thermistor and a YSI 57 oxygen probe, respectively, both apparatuses being connected to a Li Cor data logger. In addition, water temperature was measured with a mercury thermometer twice daily (8 a.m. and 3 p.m.) in the six tanks.

Integrated water samples were collected at 3 p.m. daily during the first week and every 3 days afterwards, using a PVC tube (3.4 cm in diameter and 45 cm in length) immersed vertically. The water was processed immediately after sampling. Ammonia (NH_4-N) was measured using a spectrophotometer (Koroleff, 1970). Orthophosphate (PO_4-P), and nitrates (NO_3-N) were analysed using a Technicon Auto-Analyzer (Strickland and Parsons, 1972). Bacte-

Table I. Phytoplanktonic composition, expressed as number and volume percentages, of the mixture used to initiate the tanks. Cell size is expressed as equivalent spherical diameter (ESD).

Species	Cell size (µm ESD)	Cell volume (µm^3)	% nb	% vol
Chlorophycea				
Tetraselmis sp.	8.0	268	11.6	24.2
Chlorella sp.	2.1	5	13.9	0.5
Closteriopsis sp.	7.8	245	0.5	0.9
Coenochloris sp (isolated cells)	14.2	1 502	0.3	3.8
Kirchneriella sp.	5.1	70	57.4	31.3
Monoraphidium arcuatum	4.2	40	0.1	0.0
Scenedesmus acuminatus	10.0	523	4.4	18.0
Scenedesmus obtusus	10.0	523	2.5	10.2
Westella botryoides:				
Isolated cells	5.1	69	7.5	4.1
Coenobes (8 cells)	10.2	555	1.4	6.9
Cyanophycea				
Cylindrospermum (cf) *minimum*	2.4	7	0.3	< 0.1
Oscillatoria amphigranulata	13.4	1 256	< 0.1	0.4
Diatoms				
Navicula sp.	15.3	1 874	< 0.1	< 0.1

ria direct counts were determined using epifluorescence microscopy (Porter and Feig, 1980). Bacterial production was determined from the rate of tritiated thymidine incorporation into macromolecules (Torréton and Bouvy, 1991). Chlorophyll *a* (Chl) concentrations of algae retained on Whatman GF/F filters were determined after methanol extraction (Yentsch and Menzel, 1963) using a Turner Design Fluorometer. Particle fractionation (3- and 8-µm Nuclepore membranes) gave an estimate of chlorophyll biomass for several size classes (0.7–3, 3–8 and >8 µm). Chlorophyll biomass was converted into carbon biomass using a carbon/chlorophyll ratio equal to 50. Volume (Vol) and size spectrum of particles ranging between 1.6 and 75 µm equivalent spherical diameter (ESD) were assessed using a Coulter Counter Multisizer II (70- and 280-µm orifice tubes).

2.3. Zooplankton

Zooplankton was collected at night (8 p.m.) using a PVC tube (8.4 cm in diameter and 45 cm in length, ca. 2.2 L sampled) immersed vertically at approximately 0.3 m from the tank wall and plugged on both sides. For each tank, three tubes were pooled in a bucket and sieved through a 64-µm mesh conical concentrator. Tubes, buckets and concentrators were specifically used for each species in order to avoid cross-contamination. The samples were preserved in buffered formaldehyde at 5% final concentration. Organisms were counted in the whole sample or in subsamples made volumetrically using wide bore piston pipettes (0.5–5 mL) and including at least 300 individuals. Total length excluding setae (L in mm) was measured under a dissecting microscope and converted into dry weight (W in µg) using the following relationships:

$$W = 9.0\ L^{2.76}$$

for *Moina micrura* (Saint-Jean and Bonou, 1994);

$$W = 4.42\ L^{2.55}$$

for *Diaphanosoma excisum*;

$$W = 4.8\ L^{2.63}$$

for *Thermocyclops decipiens* (*Thermocyclops* sp. from Lake Chad).

Dry weights were converted into carbon using a carbon/dry weight ratio of 0.45. For cyclopoid nauplii the different stages were not distinguished during the counting and a constant individual weight of 0.08 µg C was used (unpubl. data). For rotifers, which were contaminant species, we also adopted constant individual weights: 0.012 µg C for *Lepadella* sp. and 0.095 µg C for *Brachionus calyciflorus*.

The daily rates of increase in numbers (r = population growth rates) or in biomass (a) were calculated as the slopes of the semi-logarithmic time-numbers or time-biomass regression lines, from the initial sampling date to the day of maximal biomass. The biomass percentage (B%) that could be harvested daily during the population growth phase, without causing a population decline, was estimated from the biomass increase rate (a):

$$B\ \% = 100(\ (\exp(a) - 1)/\exp(a)\ )$$

(Bonou and Saint-Jean, 1998).

2.4. Statistical treatment

Student's paired *t*-tests were performed to compare mean values between duplicate tanks. One factor analysis of variance (ANOVA) was used to compare mean values between the six tanks.

3. RESULTS

3.1. Environmental variables

Temperature in microcosms displayed clear diel variations with a daily amplitude ranging from 0.5 to 2.5 °C and minima occurring between 6 and 8 a.m. and maxima between 4 and 6 p.m. Mean daily values ranged between 25 and 29 °C with maximal values between d7 and d11. No significant difference was found between the temperatures recorded in the different tanks (ANOVA test). Dissolved oxygen also displayed diel changes (daily amplitude from 0.2 to 4.0 $mg \cdot L^{-1}$) and showed similar variation in the two tanks where it was recorded. Mean daily concentrations increased until d4, stabilized around 6 $mg \cdot L^{-1}$ until d10 and then decreased regularly until d22 and fluctuated between 2 and 3 $mg \cdot L^{-1}$ afterwards.

For each of the other environmental variables measured, no significant differences between duplicate tanks were found (paired *t*-test, $P < 0.05$).

Nutrient concentrations showed similar changes in the three species tanks. Ammonia decreased sharply between d0 and d4, remained at low levels until d7 and then increased progressively (*figure 1a*). Nitrate concentrations decreased from d0 to d8 and then remained stable around 40 $\mu mol \cdot L^{-1}$. Phosphate concentrations increased quite linearly during the whole sequence (*figure 1b*).

Bacterial densities and thymidine incorporation peaked on d3–d4 in the *M. micrura* and *T. decipiens* tanks and on d5–d6 in the *D. excisum* tanks (*figure 2*). During this first phase, bacterial parameters were higher in the *M. micrura* tanks than in the other tanks, with a maximum density of 3.6×10^9 $cells \cdot L^{-1}$ and a maximum thymidine incorporation rate of 1.6 $nmol \cdot L^{-1} \cdot h^{-1}$. High bacterial numbers were observed during a second bacterial development phase starting from d9 in all tanks. Conversely, thymidine incorporation rates remained relatively constant, except in the *T. decipiens* tanks where an increase was noted from d13.

Chlorophyll concentrations showed similar trends in the six tanks during the first week (*figure 3a*). Their exponential increase coincided with the decrease in ammonia values (d4). From d8, a second increase to very high values (800 $\mu g \cdot L^{-1}$ on d32) was observed in the *T. decipiens* tanks. A second increase was also observed from d12 in the *D. excisum* tanks but to lower values than in the *T. decipiens* tanks. No data were recorded in *M. micrura* tanks after d12 (see below). Particle volume followed the same pattern as chlorophyll until d4, then showed a more or less stable

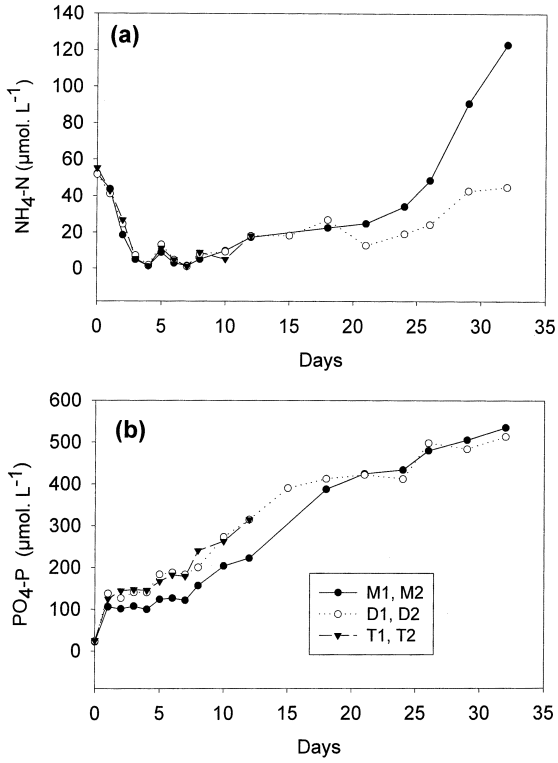

Figure 1. Time series of ammonia (a) and phosphates (b) in the tanks (average values of duplicates).

level in the six tanks (*figure 3b*). Small particles (< 8 µm), were dominant in the inoculation mixture, representing up to 60% of chlorophyll concentration and algal volume, because Chlorophycea (*Kirchneriella* sp. and *Tetraselmis* sp.) were abundant (*table I*). This size-category decreased sharply in all tanks during the first bloom (*figure 4*), reaching very low values in the *D. excisum* tanks (< 10% Chl from d2 and d10 and < 10% Vol from d5 to d32).

3.2. Zooplankton

M. micrura parthenogenetic individuals quickly developed and peaked in abundance on d5 (tank M1) or d6 (M2) (*figure 5a*). Ephipial females appeared at the population maximum and males appeared the same day (M2) or 1 day later (M1). The species had completely disappeared in both tanks on d9.

The peak in abundance of parthenogenic females of *D. excisum* occurred on d7 and was followed by a marked increase in juvenile abundance on d8 (*figure 5b*). Males appeared on d8 and remained present until d12. During the same period several females with black ovaries (probably mictic) were observed. Two other peaks of females and juveniles were observed afterwards, but featured lower abundances and longer delays between young and adult stages than for the first peak.

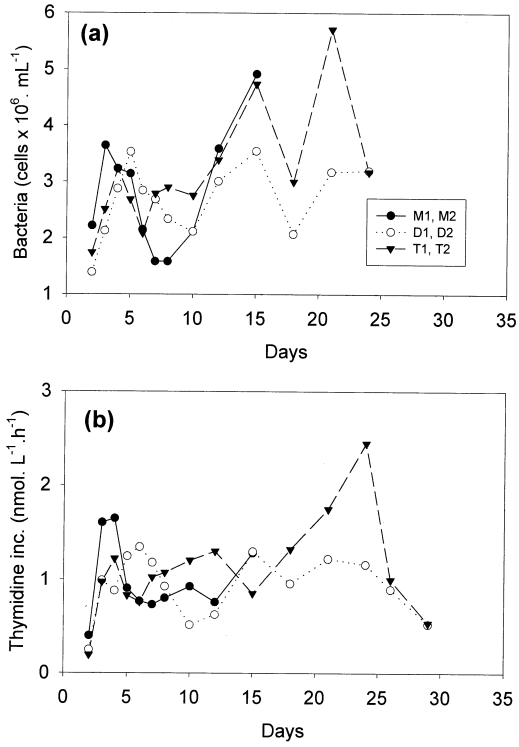

Figure 2. Time series of bacterial numbers (a) and thymidine incorporation rates (b) in the tanks (average values of duplicates).

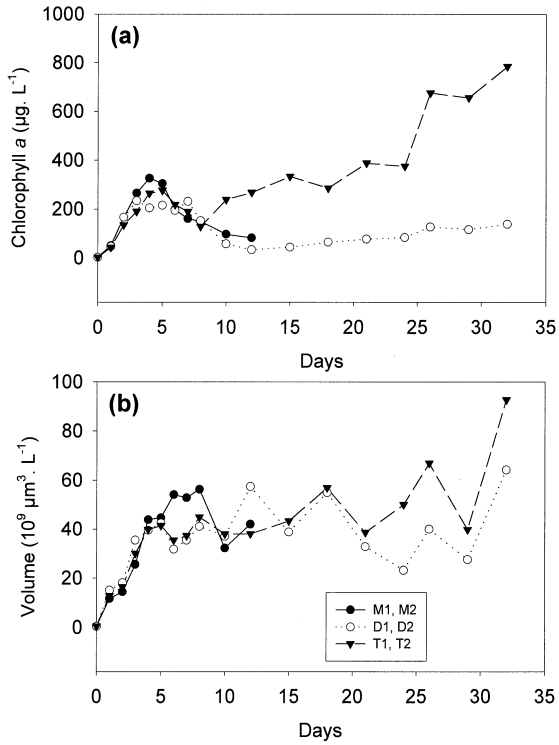

Figure 3. Time series of chlorophyll concentration (a) and particle volume (b) in the tanks (average values of duplicates).

Nauplii of *T. decipiens* had noticeable densities (9 ind.·L^{-1}) on d3, 1 day after the inoculation with zooplankton. They increased almost exponentially in both tanks until d17, then slightly decreased and increased again after d24 (*figure 6a*). Young copepodites (CI–CII) appeared on d4 (T2) or d5 (T1). Total copepodites reached their maximal density on d10 in T1 and on d17 in T2. Afterwards they decreased and reached very low densities by the end of the survey. Adults reached densities notably higher than the inoculation density (2 ind.·L^{-1}) on d6 in T2 (14 ind.·L^{-1}) and on d7 in T1 (6 ind.·L^{-1}). Their numbers increased exponentially until d12 (T2) or d15 (T1) and then fluctuated around very high densities (150–300 ind.·L^{-1}). Adults included mainly ovigerous females until d5–d6, whereas males dominated from d6 to d15 in T1 and from d6 to d9 in T2 (*figure 6b*). Afterwards, the three adult components had comparable percentages in T1, but non-ovigerous females became important from d15 in T2.

In terms of total abundance, the three species displayed an initial exponential phase (*figure 7*). During this phase, the rates of increase in numbers or biomass were much higher for *M. micrura* than for *D. excisum* and *T. decipiens* (*table II*). Although they showed the highest increase rates, *M. micrura* populations reached the lowest biomass during the colonization phase (1 100 µg C·L^{-1} against 2 000 and 1 400 µg C·L^{-1} for *D. excisum* and *T. decipiens*, respectively) and crashed afterwards. A sharp decrease also followed the initial growth phase of *D. excisum*, but it did not lead to the extinction of the population and a second (non-exponential) increase occurred after d12. The biomass of *T. decipiens*, was steady around 1 200 µg C·L^{-1} after the exponential growing phase.

Contaminant rotifers (mainly *Lepadella* sp. and *Brachionus calyciflorus*) were absent or rare during the colonization phase of the target species (*figure 7*). Their biomass increased from d5, d16 and d12 in the *M. micrura*, *D. excisum* and *T. decipiens* tanks, respectively. Rotifers became more important than the reared species only after the crash in the *M. micrura* tanks and at the end of the survey (d25–d32) in the *D. excisum* tanks.

4. DISCUSSION

4.1. Growth capacities of the three species

The mean population growth rates of the two cladocerans (1.19 d^{-1} for *M. micrura* and 0.78 d^{-1} for *D. excisum*) were higher than the values reported for the same species under similar temperature conditions in other culture systems in Côte d'Ivoire: 0.67–0.92 d^{-1} for *M. micrura* in 4-m^3 tanks (Bonou and Saint-Jean, 1998) and 0.3–0.5 d^{-1} for *D. excisum*, in

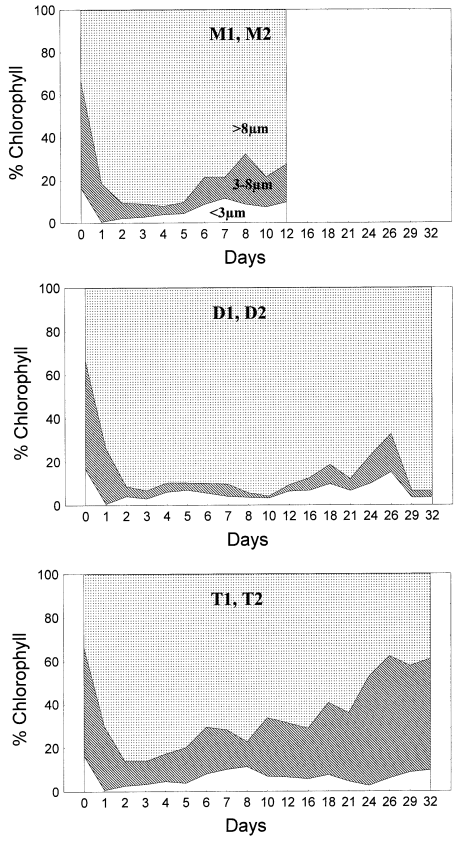

Figure 4. Time series of algal particle size-structure, expressed as percentages of total chlorophyll biomass, in the tanks (1–2: duplicate tanks for each species *Moina micrura*, *Diaphanosoma excisum* and *Thermocyclops decipiens*).

100–500-m^2 fertilized ponds (Saint-Jean and Bonou, 1994). Similar rates (1.4 d^{-1}) were reported for *M. dubia* in 10-L aquaria in Nigeria (Adeyemo et al., 1994), but a much lower value (0.4 d^{-1}) was estimated for *M. micrura* in a temporary fish pond located in Venezuela (Lopez and Theis, 1997). We found no comparative data for *T. decipiens* in the literature, but the average rate of biomass increase estimated in the present study (0.36 d^{-1}) is lower than rates found for two other cyclopid species raised in semi-controlled conditions (limed aquaculture ponds) in Côte d'Ivoire: 0.4–0.7 d^{-1} for *Mesocyclops ogunnus* (Saint-Jean and Bonou, 1994) and 0.75 d^{-1} for *Apocyclops panamensis* (Pagano et al., 1999).

Based on biomass increase rates observed during the exponential phase (*a*, *table II*), 70, 54 and 30% of the existing biomass could have been harvested each day for *M. micrura*, *D. excisum* and *T. decipiens*, respectively, without causing a population decline. These yields correspond to daily crops (if made at around three-quarters of the maximal biomass) of 261, 360 and 140 mg $C \cdot m^{-3}$, close to those obtained for *M. micrura* (250–500 mg $C \cdot m^{-3} \cdot d^{-1}$) in 4-$m^3$ tanks (Bonou and Saint-Jean, 1998).

4.2. Regulating mechanisms

The quick development of phytoplankton after inoculation was allowed by the chicken manure fertilization, as observed in other aquaculture structures (Delincé, 1992). Despite a regular fertilization, ammonium concentration quickly decreased during the first days, probably due to algal and bacterial uptake as suggested by their inverse relationships. It is known that phytoplankton are responsible for a large proportion of ammonium uptake in aquatic systems, and recent studies have clearly demonstrated that heterotrophic bacteria can also account for a large fraction of ammonium use (Kirchman, 1994). During the first days of the survey, development of heterotrophic bacteria was probably linked to the available dissolved substrates in the chicken manure. Variation in bacterial numbers was concomitant with phytoplankton development, suggesting that phytoplankton products are important substrates for bacterioplankton growth, as demonstrated in other freshwater systems (Bouvy et al., 1998). Decrease in bacterial density may have resulted from the concurrent development of heterotrophic nanoflagellates, as observed in a tropical pond in Côte d'Ivoire (Guiral et al., 1994). The collapse of the algal bloom was probably partly due to NH_4-N limitation, despite the fact that NH_4-N levels did not reach very low concentrations (around 2 $\mu mol \cdot L^{-1}$ on d4). In the *T. decipiens* tanks, phytoplankton increased again immediately after the collapse of the first bloom, coinciding with the increase of the bacterial parameters. In the cladoceran tanks, the control of phytoplankton (particularly in the < 8-µm size classes) was probably mainly exerted through selective grazing pressure. This suggestion is reinforced by the fact that cladocerans generally have a higher impact on nanophytoplankton than cyclopoids (Pourriot et al., 1982).

M. micrura numbers quickly increased, but the population crashed just after the maximal density was reached. This crash was accompanied by a shift from parthenogenetic to sexual reproduction. Many factors are likely to induce a reproductive shift in cladocerans, such as photoperiod, temperature, food and chemically mediated cues (Pourriot et al., 1982). In our study, temperature and photoperiod effects can be excluded. Food limitation and accumulation of metabolic products, which are both density-dependant factors, are often associated (Kleiven et al., 1992). Before and during the crash of the *M. micrura* population, the food level remained high, with chlorophyll concentrations around 200–300 $\mu g \cdot L^{-1}$. The small algae (< 8 µm), which were probably more easily ingested than the large ones which included algal colonial species, corresponded to a carbon biomass around 1.5–2 $mg \cdot L^{-1}$, which is ten-fold higher than the threshold food concentrations (i.e. minimum food to allow production) for tropical cladocerans, estimated around 0.1–0.2 mg $C \cdot L^{-1}$ (Duncan, 1989). Therefore, food limitation was probably of lower importance than crowding to initiation of sexual reproduction in *M. mi-*

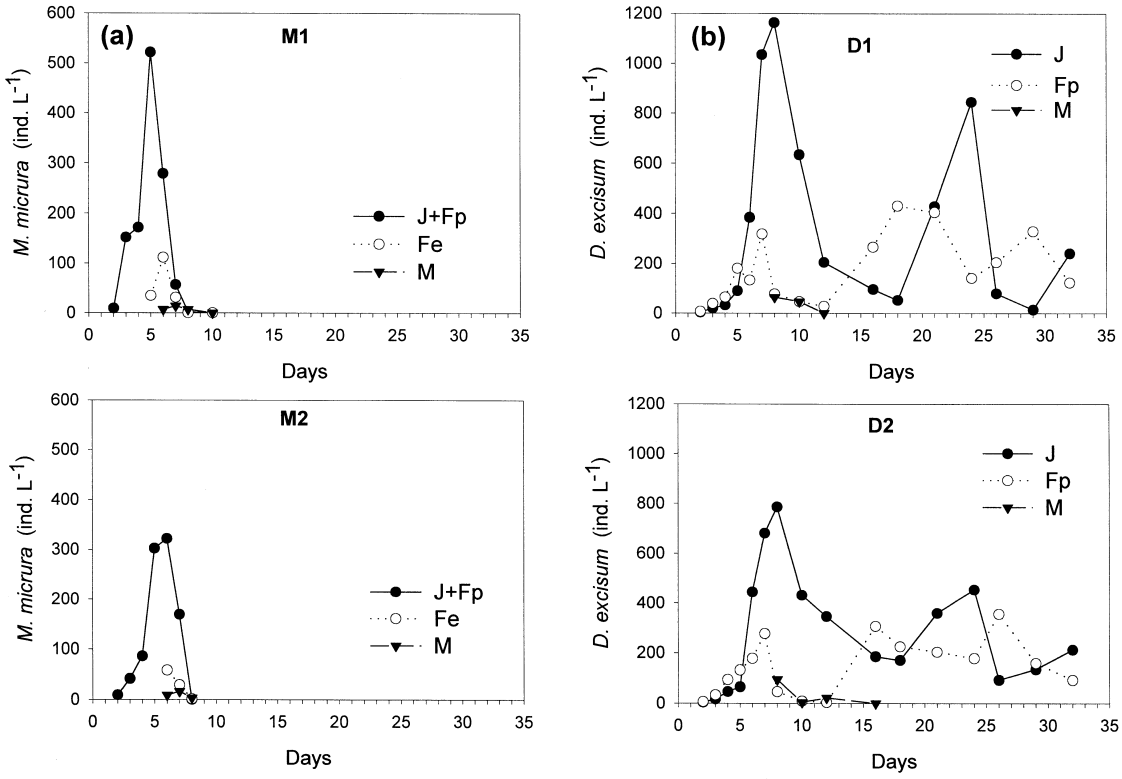

Figure 5. Time series of the densities of the cladocerans: *Moina micrura* (a) and *Diaphanosoma excisum* (b). J, juveniles, Fp, parthenogenetic females, Fe, ephippial females, M, males. 1–2: duplicate tanks for each species *Moina micrura*, *Diaphanosoma excisum* and *Thermocyclops decipiens*.

crura, or it occurred at an unusually high food threshold. Furthermore, the shift to sexual reproduction occurred at densities (300–500 ind.·L^{-1}) much lower than densities observed elsewhere for the same species [e.g. 6 000 ind.·L^{-1} (Bonou and Saint-Jean, 1998)]. This difference could result from a genetic adaptation to crowding and high food conditions as evidenced elsewhere for the rotifer *Brachionus plicatilis* (Carmona et al., 1993). Indeed, the animals used for these experiments were previously grown for multiple generations in low volume structures under very high food conditions (see Methods), which could have favoured and selected populations having low density and high food thresholds.

D. excisum numbers decreased and the population shifted to sexual reproduction after the population maximum. However, in contrast to *M. micrura*, they did not crash and the shift to sexuality was only partial. A high proportion of parthenogenetic individuals was recorded until the end of the survey. Population regulation processes were probably related to food limitation. Indeed, if the total phytoplankton biomass remained high (> 1.5 µg C·L^{-1}) during the decreasing period of *D. excisum* population (d7–d12), the < 8 µm algal biomass reached values (0.15 mg C·L^{-1} on d10–d12) in the range of the threshold food concentration for tropical cladocerans (Duncan, 1989). In addition, we know from laboratory grazing experiments with natural algal food (Pagano and Saint-Jean, unpubl.) that this species feeds primarily on small particles (size < 8–9 µm), in agreement with results reported for the congener *D. brachyurum* (Bern, 1994). In the present study, small particles were quickly depleted during the first days in *D. excisum* tanks, probably due to selective grazing pressure on *Kirchneriella* sp., which led to a food limitation.

In *T. decipiens* tanks, the firsts adults issued from ovigerous females inoculated on d2 appeared on d6–d7, which means that minimal juvenile development time was around 4–5 days, i.e. slightly lower than the mean values reported by Gras and Saint-Jean (1981) for *T. neglectus* (5.8–6.2 days, at 30 °C). This quick development and high proportions of ovigerous females explained the quick and exponential increase of nauplii, copepodite and adult numbers in the tanks at the beginning of the survey. After this initial phase, the number of nauplii continued to increase but at a slower rate, that of the adults had no clear trend but remained high and that of copepodites declined down to very low values. This large decrease in copepodite density could have resulted from moulting failures (e.g. N6–C1) or increased stage-specific mortality in relation to: a) food (i.e. decreasing food abundance and increasing competition with contaminant rotifers);

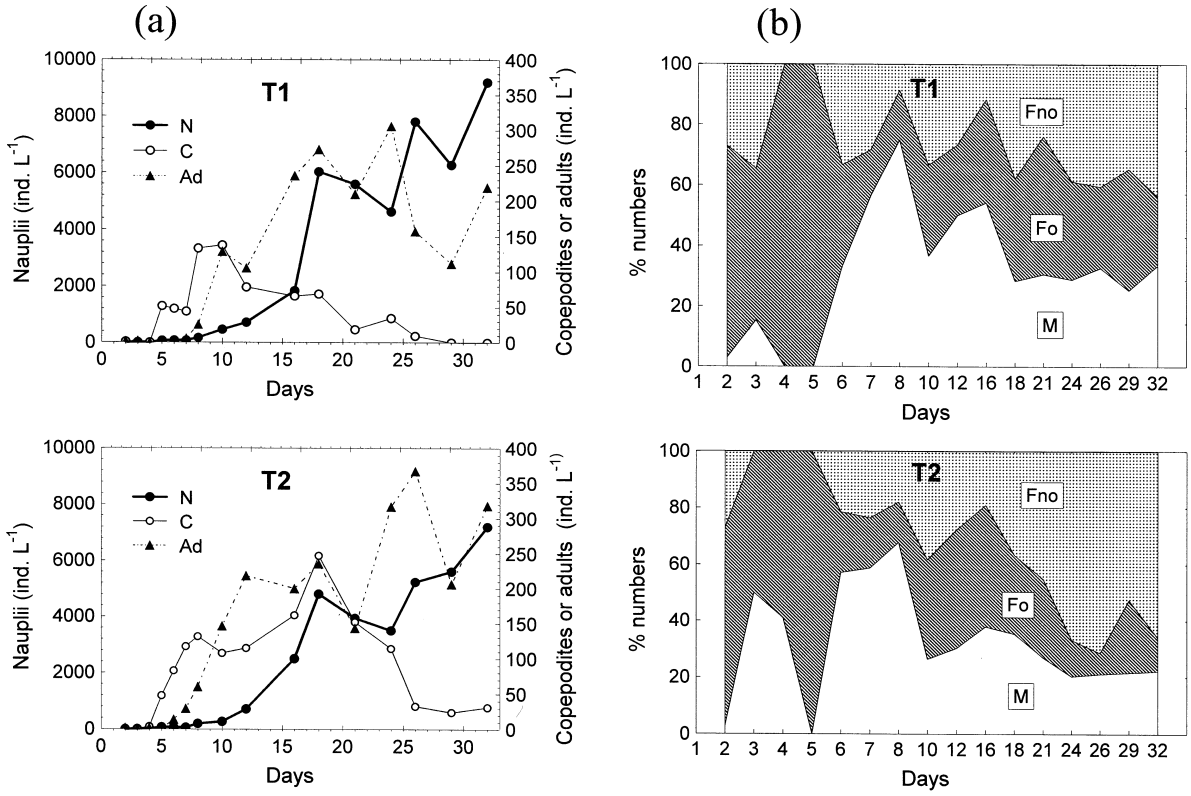

Figure 6. Time series of the densities of nauplii (N), copepodites (C) and adults (Ad) of *Thermocyclops decipiens* (a) and percentages of males (M), ovigerous females (Fo) and non-ovigerous females (Fno) among the adult numbers (b). 1–2: duplicate tanks for each species *Moina micrura*, *Diaphanosoma excisum* and *Thermocyclops decipiens*.

b) predation by adults or late copepodites; and c) degradation of abiotic conditions (e.g. pH or oxygen). The food limitation hypothesis is weak because the algal biomass in the < 8-µm size fractions (ca. 4 mg $C{\cdot}L^{-1}$), which is probably the most available to young stages, remained much higher than the food thresholds reported for naupliar development of *Cyclops vicinus* (0.5 mg $C{\cdot}L^{-1}$) and *Mesocyclops leuckarti* (0.3 mg $C{\cdot}L^{-1}$) by Hansen and Santer (1995). Competition with rotifers is not clear because rotifer biomass in tank T1 was ten time lower than cyclopid biomass when copepodite numbers began to decrease (d10). Predation control through cannibalism by older copepodites and adults, which are known to be primarily carnivorous, is a more realistic explanation. Indeed, at the beginning of the decrease in copepodite abundance, rotifer biomass (around 0.1–0.3 mg $C{\cdot}L^{-1}$) was insufficient to fulfil the food requirement of adults (including 20–40 % of ovigerous females) if we refer to the food threshold for egg production for *C. vicinus* (0.5 mg $C{\cdot}L^{-1}$) reported by Santer and Vandenbosch (1994). Concerning the abiotic factors, we have no data on pH, and the role of dissolved oxygen is questionable because concentrations were still high (around 6 $mg{\cdot}L^{-1}$) when copepodites began to decrease in tank T1.

5. CONCLUSION

The three investigated species displayed high growth capacities in monospecific cultures confirming their appropriateness for aquaculture. The two cladocerans, *Moina micrura* and *Diaphanosoma excisum*, had distinctly better performances than the copepod *Thermocyclops decipiens.*

The three species showed different regulating factors in culture conditions.

— *M. micrura* seemed mainly controlled by crowding in relation to chemical cues, which probably do not have the same effects in natural or renewed environments as they did in the stagnant waters of the present work.

— *D. excisum* seemed mainly controlled by the availability of small food particles. This characteristic is probably also very important in natural conditions and should be considered when examining structuring factors of zooplankton communities.

— *T. decipiens* appeared mainly regulated through the predation exerted by the older stages on the younger ones, but this process is certainly less important in natural conditions where other potential prey are available.

Table II. Population growth rates (*r*) and biomass increase rates (*a*) calculated from the sowing day (t_0 = d2) to the day of maximal biomass (t_1). n, number of pairs; R, correlation coefficient for the time-number or time-biomass regression lines. R significant at $P < 0.05$ (*), $P < 0.01$ (**), $P < 0.001$ (***) or non-significant (ns).

Species	Tank	t_1	n	$r \pm$ SD (d^{-1})	R	$a \pm$ SD (d^{-1})	R
M. micrura	1	5	4	1.24 ± 0.36	0.921 ns	1.25 ± 0.37	0.922
	2	5	4	1.14 ± 0.10	0.994 ***	1.13 ± 0.10	0.993 ***
	mean	5	4	1.20 ± 0.28	0.948 *	1.19 ± 0.28	0.949 *
D. excisum	1	7	6	0.81 ± 0.08	0.973 ***	0.79 ± 0.06	0.988 ***
	2	7	6	0.75 ± 0.10	0.959 ***	0.76 ± 0.07	0.984 ***
	mean	7	6	0.78 ± 0.09	0.970 ***	0.77 ± 0.05	0.990 ***
T .decipiens	1	18	11	0.37 ± 0.12	0.730 *	0.37 ± 0.06	0.886 ***
	2	18	11	0.46 ± 0.12	0.791 **	0.36 ± 0.06	0.891 ***
	mean	18	11	0.45 ± 0.12	0.781 **	0.36 ± 0.05	0.914 ***

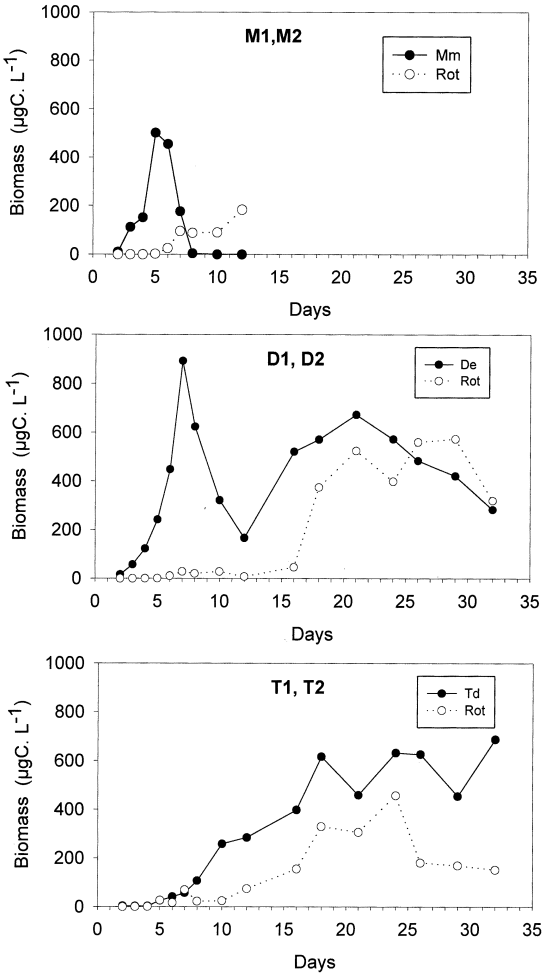

Figure 7. Time series of *Moina micrura* (Mm), *Diaphanosoma excisum* (De), *Thermocyclops decipiens* (Td) and contaminant rotifers (Rot) biomass in the tanks (average values of replicates). 1–2: duplicate tanks for each species *Moina micrura*, *Diaphanosoma excisum* and *Thermocyclops decipiens*.

Knowledge of these regulating factors can help to improve the zooplankton production in culture. For example, the yield could be distinctly increased by regularly cropping larger size-classes which could reduce a) crowding for *M. micrura*, b) grazing pressure for *D. excisum* and c) adult predation for *T. decipiens*. Other ways to improve the yields are to ensure a water replacement, especially in the case of *M. micrura* to reduce metabolite accumulation.

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