

## Production biology of copepods and cladocerans in three south-east Sri Lankan low-land reservoirs and its comparison to other tropical freshwater bodies<sup>†</sup>

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Received 30 April 1997; in revised form 14 May 1997; accepted 15 May 1997

**Key words:** microcrustacean zooplankton, tropical limnology, biomass, production, empirical relationships

### Abstract

Production, biomass and productivity of the microcrustacean zooplankton populations of three low-land reservoirs, Tissawewa (eutrophic), Ridiyagama (moderately eutrophic), and Muruthawela (mesotrophic) in South-east Sri Lanka were studied. The temporal variation of zooplankton production was studied in Tissawewa on basis of fortnightly sampling on five fixed sampling stations for 2 years. Zooplankton production was relatively high, mainly because of high copepod production predominantly realised due to two calanoid copepods, *Phyllodiaptomus annae* and *Heliodiaptomus viduus*. About half of the copepod production was contributed by the naupliar instar stages, whereas the contribution of the eggs was generally much smaller (<20%). In contrast, the cladoceran production consisted for ca 50–70% of egg production. The results of this study were compared with those from more than twenty other tropical and subtropical waterbodies reported in the literature by deriving empirical relationships between mean phytoplankton biomass and mean zooplankton biomass and production. Mean zooplankton biomass and annual zooplankton production were found to be positively related to mean phytoplankton biomass, and mean phytoplankton biomass proved to be a good predictor of mean zooplankton biomass ( $r^2 = 0.58$ ) and a moderate good predictor of annual zooplankton production ( $r^2 = 0.43$ ). However, the relationships between the mean phytoplankton biomass and zooplankton P/B were not significant neither for small-bodied and large-bodied cladocerans nor for copepods.

### Introduction

Compared with the temperate regions, limnology of the tropics is still in its infancy. Although a large amount of literature on tropical inland waters has now accumulated there are few comprehensive studies which has been carried out over a longer period of time. Even current research is mainly directed to taxonomy and making inventories of species. Tropical lakes differ in at least two fundamental properties from temperate lakes: high annual irradiance, and low daily and annual

variations in irradiance (Lewis, 1987). These result in a limited number of effects, of which high water temperature, low variation in water temperature, and high primary production are the most important in regard to secondary production.

Secondary production estimates are useful indications of the functional role of invertebrates in any ecosystem. They measure energy or organic matter flow within communities, they are a measurement of the success of a species in a given community or ecosystem, and they present a link between population and ecosystem ecology (Benke, 1993). The published information on zooplankton production in the

<sup>†</sup>Publication no. 2269 of the Netherlands Institute of Ecology, Centre for Limnology.

tropical region is meagre. This is because measuring secondary production in the tropical region is generally a hard and difficult task which needs quantitative sampling, and good culture and data processing facilities. As the zooplankton populations in tropical regions are continuously recruiting and growing, the more direct, and, therefore, more simple cohort approach cannot be used (Rigler & Downing, 1984). Instead, apart from the field data on density, population structure and fecundity, independent information on growth and recruitment is needed. This requires culturing the animals under conditions of food and temperature similar to those in nature, as well as a detailed analysis of the life history responses of the studied species (Vijverberg, 1989; Anderson & Benke, 1994).

In the tropics, size of pelagic microcrustacean zooplankton is generally smaller than in the temperate region (see for a review in Fernando, 1980). The reason for this is at present not clear. It may be due to one or more factors, such as: the effects of high and uniform temperatures, food limitation, and intensive positive size selective predation by fish.

In this paper we present a detailed study of the production biology of the microcrustacean populations of three contrasting South-east Sri Lankan low-land reservoirs: Tissawewa (ancient, shallow, eutrophic), Ridiyagama (recent, shallow, moderately eutrophic), and Muruthawela (new, deep, mesotrophic). The study had two objectives: (1) to describe in detail on a species basis the temporal variations in biomass, production and productivities of the microcrustaceans in Tissawewa; and (2) to compare these with those data from the two other Sri Lankan reservoirs, Ridiyagama and Muruthawela, and other tropical and subtropical waterbodies of varying trophy.

## Methods

### *Study area*

The three reservoirs are located in the dry-zone of Sri Lanka. Two monsoon periods occur annually in the southern and eastern low-lands of the country. The major rainy season is during the north-east monsoon in November, and a minor rainy period occurs during the south-west monsoon in May. The low-land reservoirs studied belong to three different river basins. Their main function is storage of water for irrigation purposes. Tissawewa (location: 6° 18' N, 81° 17' E) is the oldest (35 AD) and the smallest (surface area: 250 ha) of

the three reservoirs. It is very shallow ( $Z_{\text{mean}} = 1.7$  m;  $Z_{\text{max}} = 3.5$  m), wind exposed, and characterized by strong waterlevel fluctuations. The water is eutrophic, mean gross primary production amounts to 9.5 g O<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup> (Piet et al., in press). In July 1992 at the end of the dry season, an extreme drought caused water levels to drop drastically, making routine sampling impossible. During September almost the whole reservoir dried up, with the first NE monsoonal rains in October it started filling up again. Therefore, it was not sampled before November. Ridiyagama reservoir (location: 6° 13' N, 80° 59' E) was impounded in 1923 and is the largest (surface area of 888 ha) of the three reservoirs. It is moderately eutrophic, shallow ( $Z_{\text{mean}} = 3.0$  m;  $Z_{\text{max}} = 5.3$  m), wind exposed, but compared with Tissawewa has moderate water level fluctuations. Muruthawela (location: 6° 13' N, 80° 43' E) was constructed in 1968, is of intermediate size (mean surface area: 520 ha), mesotrophic, and is the deepest ( $Z_{\text{mean}} = 9.1$  m;  $Z_{\text{max}} = 36.0$  m) of the three reservoirs. In contrast to the other two reservoirs, it has a dendritic shape and exhibits low water level fluctuations.

### *Sampling methods*

Muruthawela and Ridiyagama reservoirs were sampled fortnightly, from May 1988 to September 1988, and Tissawewa from October 1990 to December 1992. Copepods (copepodite stages) and cladocerans were sampled quantitatively with a 12 l Schindler volume-sampler, and nauplii with a 3 l Ruttner bottle. The samples were filtered through plankton gauze, 80 µm mesh to retrieve the copepods and cladocerans and 30 µm mesh sieve to collect the nauplii, and preserved in 4–5% formalin. Each reservoir was sampled at five fixed stations, which were evenly distributed over the open-water zone. In Muruthawela, at each station five samples were collected from five different relative depths: a sample each just below the surface (relative depth 0.0) and just above the bottom (relative depth 1.0), and at relative depths of 0.25, 0.50 and 0.75. In Ridiyagama and Tissawewa sampling was carried out at three relative depths from each of the stations: below surface, at intermediate depth, and above the bottom.

Qualitative samples were collected at one fixed station, using plankton nets with mesh sizes of 120 and 335 µm mesh. Samples were preserved in 98% ethanol (final concentration 60–80%) and stored in the refrigerator to prevent loss of eggs.

### Evaluation of samples

Quantitative samples were used to measure densities, size frequency distributions and instar distributions, while qualitative samples were used to estimate for each species separately: size at maturity (Cladocera), proportion of adult females with eggs (Cladocera, Copepoda), number of eggs per clutch in relation to the size of the female (Cladocera), and number of eggs per female (Copepoda). Length was measured under the microscope with an eye-piece micrometer to the nearest 0.025 mm. Cladocerans were measured from the top of the head to the base of the tail spine, and the copepodite instars from the anterior end of the cephalothorax to the tip of the furcal rami.

### Estimation of individual biomass

The carbon content of zooplankters was measured with a UNICARB carbon analyser (Salonen, 1979) at the Netherlands Institute of Ecology, Center for Limnology (Nieuwersluis). As freeze-drying is a reasonably good method of fixation and preservation of zooplankton (Boersma & Vijverberg, 1994a), fresh living animals from Tissawewa were freeze dried at the Dept. of Zoology of the Ruhuna University (Matara). However, the lyophilized animals were badly damaged and were therefore not used for the determination of individual weight in relation to size. Instead, animals from Tissawewa, collected on 05-01-92, 31-12-92 and 10-02-93 and preserved in 4% formalin were used.

Omori (1978) demonstrated the leaching effects of 4% formalin as preservative: a significant decline in the dry weight of marine copepods. Salonen & Sarvala (1985) found that preservation with formaldehyde resulted in a rapid loss of about 35% of carbon. Schram et al. (1981) showed that *Ceriodaphnia lacustris* preserved in 3% formalin exhibited a maximal loss of dry weight within the first sixty days of preservation and that additional loss after 60 days was almost zero.

The weight losses of microcrustaceans as the result of preservation in 4% formalin were assessed for crustacean zooplankton collected from Lake Loosdrecht in The Netherlands. Part of the sample was analysed for carbon content immediately after collection, the rest preserved in 4% formalin. After 60 days animals from the preserved samples were analysed for carbon content and compared with the carbon content of fresh, non-preserved animals measured directly on collecting. Correction factors of weight loss were calculated, they usually varied between 15 and 35%. These correc-

tion factors were applied to correct the carbon contents of the microcrustacean species involved in the present study.

Length-weight relationships were calculated using the linearized form of the relationship:

$$W = aL^b,$$

where  $W$  = weight of animals in mg dry weight,  $a$  = intercept,  $b$  = slope and  $L$  = length of animal in mm. For copepods four length-weight relationships were determined: for cyclopoid nauplii, cyclopoid copepodites, calanoid nauplii and calanoid copepodites; for each cladoceran species such regression relationships were determined, one each for individuals with eggs and without eggs. The latter was used for the calculation of somatic production.

### Production estimation

The growth-increment summation model (Winberg, 1971a) was used to estimate the microcrustacean zooplankton production. Many workers studying zooplankton populations in both temperate and tropical regions, have used the growth-increment summation model because of its simplicity and its applicability to populations without cohorts (e.g. Vijverberg & Richter, 1982a, b; Leveque & Saint-Jean, 1983; Mavuti, 1994; Vareschi & Jacobs, 1984). With this approach field data on population densities, population structure and fecundity can be integrated, with the laboratory data on development- and growth rates and length-weight relationships in order to calculate production. This was done for the four most abundant species each for copepods and cladocerans, which together contributed >98% to the total microcrustacean biomass in the three reservoirs.

The production of the whole population can be regarded as the sum of the production of the different size classes. This is obtained by the summing the products of the weight increase of the individual size classes with the respective population density. For calculating the somatic production, the formula of Pechen and Shushkina (Winberg et al., 1971a) was used:

$$P = \sum_{i=1}^n P_i = \sum_{i=1}^n \Delta W_i \cdot N_i,$$

where  $P$  = biomass production of the total population per day;  $P_i$  = biomass production of the  $i$ -th size class per day;  $n$  = the number of size classes in the popula-

tion;  $\Delta W_i$  = weight increment per day of the  $i$ -th size class; and,  $N_i$  = population density of  $i$ -th size class.

In the laboratory copepods and cladocerans were cultured individually on fresh pond water filtered through plankton gauze (mesh 50  $\mu\text{m}$ ), keeping the food constant at 10  $\mu\text{g}$  (range: 8–12 mg) chlorophyll- $a$   $\text{l}^{-1}$  (Amarasinghe et al., 1997). This food level is comparable with that in Tissawewa and Ridiyagama, but was ca 3 times higher as in Muruthawela (Amarasinghe, unpubl.). Each individual copepodite instar stage was taken as a size class for the production estimates. The instar durations required for calculation of growth rates were obtained by direct measurements in laboratory cultures, for one of the cyclopoid species (*Mesocyclops thermocyclopoidea*), and for one of the calanoid species (*Heliodyptomus viduus*) (Amarasinghe et al., in press). Since the other two species, *Thermocyclops decipiens* and *Phylloodyptomus annae*, were not present in the reservoir at the time the culture experiments were carried out, the instar durations of these species were indirectly estimated. Instar durations for *T. decipiens* and *P. annae* are based on those of *Mesocyclops thermocyclopoidea* and *Heliodyptomus viduus*, respectively: by using the ratios of the individual biomass of adult females.

The copepod growth in length increment per moult was estimated from the mean length of the nauplii and copepodite instars in the field population at the time. Somatic weight of each instar was obtained from the length–weight relationships. Total weight per instar, and weight increments at each moult were calculated. These data enabled us to get the standing crop of somatic biomass and production of somatic biomass per unit of time. The biomass of individual eggs was assumed to be equal to the biomass of individual nauplii in their first instar. This information was used for the estimation of the standing crop biomass of eggs and for egg biomass production. Egg production was added to the somatic production to get total biomass production, and egg biomass to the somatic biomass to get total biomass.

Production of four cladoceran species, *Ceriodaphnia cornuta*, *Moina micrura*, *Diaphanosoma excisum*, and *Diaphanosoma modigliani* was estimated. For the calculation of production, the field data on densities, population structure and fecundity were combined with the laboratory observations on length growth and durations of development of eggs and instars in relation to food and temperature (for results on growth and duration see Amarasinghe et al., in press). The main difference in the method of calculating production of

cladocerans and copepods is that in the former case size classes (Table 1) were used, whereas in latter case instar classes were used.

#### *Empirical relationships*

For literature comparisons we collected published data on biomass of phytoplankton and zooplankton, zooplankton production, and of P/B ratios of different zooplankton species. These data were log-log or linear-log transformed to derive linear regressions. Model I least-squares regression analysis (Sokal & Rohlf, 1995: p. 455) was performed to test the hypothesis whether the zooplankton biomass, production, and P/B ratios could be predicted from the mean phytoplankton biomass. The relationship between phytoplankton biomass and zooplankton P/B was analysed both at the zooplankton community level and at the species level. Besides temperature, P/B is strongly related to body-size (Banse & Mosher, 1980; Roff & Tremblay, 1984; Plante & Downing, 1989) and is generally lower for copepods as compared with cladocerans (Morgan et al., 1980). Therefore, we investigated three categories: large-bodied cladocerans, small-bodied cladocerans, and copepods. Generally, phytoplankton biomass estimates in literature are reported as chlorophyll- $a$  concentrations per unit of volume, but occasionally also as fresh weight, cell volume, or dry weight. For data in units other than mg dry wt  $\text{m}^{-3}$  we derived the phytoplankton biomass converting chlorophyll to dry wt using a ratio of 1:50 between them (Baily-Watts, 1974), and carbon to dry wt using a ratio of 1:2 between these parameters (Winberg et al., 1971b) and fresh wt by taking a ratio of 10:1 (Winberg et al., 1971b). The mean chlorophyll concentration was measured in the epilimnion, most studies did not state whether chlorophyll- $a$  concentrations were corrected for phaeopigments. Most values were based on fortnightly or monthly sampling for 6 to 12 months.

Zooplankton biomass and production estimates in literature were generally expressed as mg dry wt  $\text{m}^{-3}$ , but in a few cases as fresh weight or carbon content. The values were converted to mg dry wt  $\text{m}^{-3}$  as follows: 10 g fresh wt = 1 g dry wt, and 1 g dry wt = 0.5 g carbon (Winberg et al., 1971b). The biomass data were usually based on means of fortnightly or monthly sampling for 6–12 months with a volume sampler. If production estimates were based on periods of shorter than 12 months the data were extrapolated in order to express these values in terms of annual production (12 months). For Tissawewa, biomass, production and

Table 1. Size classes (Sc, mm) of the cladoceran species used in the analyses of the production.

Species	Sc 1	Sc 2	Sc 3	Sc 4	Sc 5	Sc 6
<i>Ceriodaphnia cornuta</i>	<0.25	0.25–0.29	0.30–0.34	0.35–0.39	0.40–0.44	>0.45
<i>Moina micrura</i>	<0.30	0.30–0.39	0.40–0.49	0.50–0.59	0.60–0.69	>0.70
<i>Diaphanosoma excisum</i>	<0.40	0.40–0.49	0.50–0.59	0.60–0.69	0.70–0.79	>0.80
<i>Diaphanosoma modigliani</i>	<0.45	0.45–0.59	0.60–0.74	0.75–0.89	0.90–1.04	>1.05

productivity (P/B) were calculated for two periods: (1) October 1990 until September 1991 (12 months), and (2) October 1991 until July 1992 (9 months). Literature values of P/B for microcrustacean spp. are based on day, month, year, but we converted them all to daily P/B ratios for comparisons. If for certain lakes/reservoirs data for consecutive years were available, and if environmental conditions in these years were roughly similar, we combined these data.

## Results

### Length-weight relationships

Conversion factors were established between the carbon content of fresh and preserved zooplankton for cladocerans, cyclopoid copepods and calanoid copepods (Table 2). In case of cyclopoid copepods mean weight with and without preservation could be directly calculated because individuals of almost the same size were used for the analysis: cyclopoid copepod fresh  $0.49 \pm 0.04$  mm, and cyclopoid copepod formalin  $0.49 \pm 0.03$  mm (mean length  $\pm$  SD). In case of cladocerans and calanoid copepods first a length-weight regression was calculated, and using this relationship the mean weight for a specific length (= grand mean length) was computed (Table 2). The four regressions were highly significant: calanoid copepods fresh ( $N = 28$ ;  $r^2 = 0.80$ ;  $P < 0.001$ ), calanoid copepods formalin ( $N = 53$ ;  $r^2 = 0.90$ ;  $P < 0.001$ ), cladocerans fresh ( $N = 47$ ;  $r^2 = 0.75$ ;  $P < 0.001$ ), and cladocerans formalin ( $N = 60$ ;  $r^2 = 0.89$ ;  $P < 0.001$ ). The carbon lost due to preservation was very similar for the calanoid and cyclopoid copepods (18–19 %), but the cladocerans increased slightly in weight (ca 3%).

The length-weight relationships for cladocerans and copepods, corrected for carbon loss or gain due to formalin preservation, are given in Table 3. Slopes of regression lines of the cladocerans with eggs and without eggs were species wise compared and tested for parallelism using a sub-routine of the ANOVA-MANOVA

routine of Statistica (Statsoft, 1992). In the analysis we used individuals with and without eggs as the independent variable, weight as the dependent variable, and length as the co-variable. The slopes of the length-carbon relationships of the cladocerans with eggs and without eggs differed only significantly for *C. cornuta*, being steeper for the animals with eggs ( $F = 36.5$ ;  $df = 1,53$ ;  $P < 0.001$ ). Non-significant different slopes were observed for *M. micrura* ( $F = 1.5$ ;  $df = 1,62$ ;  $P = 0.23$ ), *D. excisum* ( $F = 3.1$ ;  $df = 1,34$ ;  $P = 0.088$ ), and *D. modigliani* ( $F = 1.1$ ;  $df = 1,45$ ;  $P = 0.30$ ).

### Biomass, production, and P/B estimates for the zooplankton in Tissawewa

The daily production estimates of the four cladoceran species ranged from almost zero to  $50 \text{ mg C l}^{-1} \text{ d}^{-1}$  for *C. cornuta* in November and December of 1992 (Figure 1). The P/B ratios, however, were more stable, with some exceptions for *C. cornuta*: averaged around 0.25 for both the *Diaphanosoma* spp. But for the two smaller cladocerans values generally ranged between 0.25 and 1.0, and for *C. cornuta* even ratios  $> 1.0$  were encountered during some periods of the year. The relative contributions of the different size classes of the cladoceran species to production differed (Figure 2). The production of the smallest cladoceran *C. cornuta* could be mainly attributed to the eggs (70%), whereas for the three larger species the contribution of the eggs to the total production was somewhat less (mean ca 50%). The temporal variation in the egg production as proportion of the total production is high. All four species showed periods with zero egg production; especially for *D. excisum* longer periods were observed with low egg production. Just after the drought in 1992 the proportion of egg-production to the total production was relatively high for all the three cladoceran species present. The total production of the cladocerans ranged from about  $2 \text{ mg C l}^{-1} \text{ d}^{-1}$  in early 1991 to ca  $15 \text{ mg C l}^{-1} \text{ d}^{-1}$  in early 1992. Just after the drought in December 1992 the densities and hence production of

Table 2. Mean Carbon lost per individual of mean length, absolute ( $\mu\text{g C}$ ) and as percentage of fresh carbon weight, as the result of formalin preservation. Also given, mean length ( $L_{\text{mean}}$ , mm), number of observations ( $N$ ), and mean weight ( $W$ ,  $\mu\text{g C}$ ).

Taxa	Fresh			Formalin		C lost	
	$L_{\text{mean}}$	$W$	$N$	$W$	$N$	$\mu\text{g C}$	%
<i>Mesocyclops leuckarti</i>	0.49	1.72	21	1.38	43	0.34	+19.8
<i>Eurytemora affinis</i>	0.70	0.37	28	0.30	53	0.07	+18.2
<i>Daphnia galeata</i>	1.33	0.89	47	0.93	60	-0.04	-3.1

Table 3. The length-weight relationships for cladocerans and copepods, corrected for carbon loss or gain due to formalin.  $W = aL^b$  ( $W$  = carbon content in  $\mu\text{g C}$ ;  $L$  = length in mm). Adult cladocerans with eggs and juveniles without eggs.

Species/Taxa	$N$	$a$	$b$	$r^2$	$P$	
<i>Ceriodaphnia cornuta</i>	with eggs	20	61.32	4.87	0.68	<0.001
	without eggs	37	0.93	1.21	0.85	<0.001
<i>Moina micrura</i>	with eggs	33	2.73	2.98	0.91	<0.001
	without eggs	33	1.21	2.70	0.91	<0.001
<i>Diaphanosoma excisum</i>	with eggs	21	1.25	1.71	0.83	<0.001
	without eggs	17	0.71	1.34	0.91	<0.001
<i>Diaphanosoma modigliani</i>	with eggs	25	1.16	1.63	0.90	<0.001
	without eggs	24	0.47	1.45	0.86	<0.001
calanoid nauplii	36	0.76	0.58	0.94	<0.001	
calanoid copepodites	77	3.36	1.69	0.95	<0.001	
cyclopoid nauplii	44	0.79	1.30	0.88	<0.001	
cyclopoid copepodites	49	1.50	1.85	0.89	<0.001	

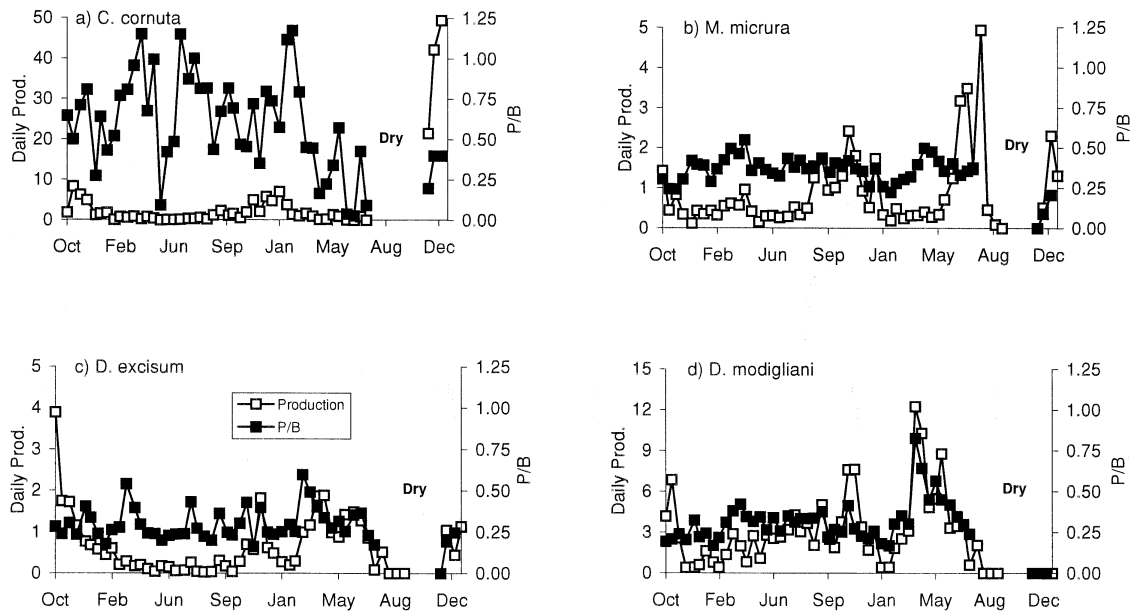


Figure 1. Daily production ( $\text{mg C l}^{-1} \text{d}^{-1}$ ) and daily P/B ratios of four cladoceran species in Tissawewa over the period October 1990 until December 1992: (a) *Ceriodaphnia cornuta*, (b) *Moina micrura*, (c) *Diaphanosoma excisum*, (d) *Diaphanosoma modigliani*. 'Dry' indicates drought period. Note the different scales for production.

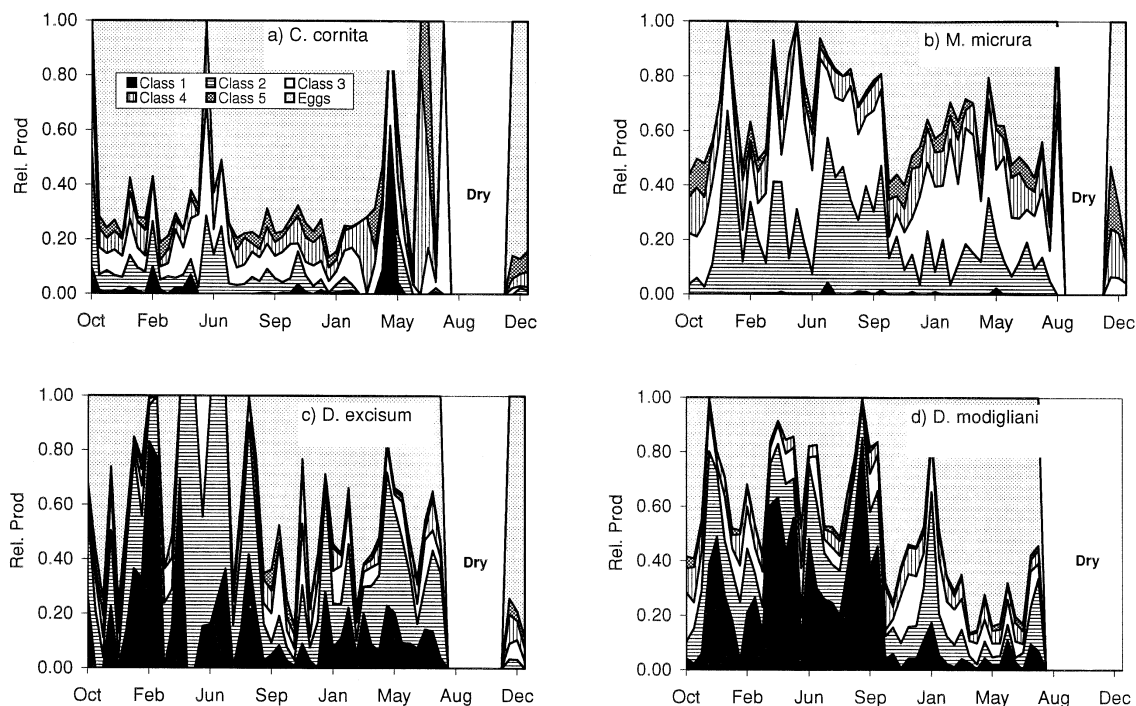


Figure 2. Relative contribution to the total production of different size classes and eggs of (a) *Ceriodaphnia cornuta*, (b) *Moina micrura*, (c) *Diaphanosoma excisum*, (d) *Diaphanosoma modigliani*, in Tissawewa over the period October 1990 until December 1992. Size classes are defined in Table 1. 'Dry' indicates drought period.

*C. cornuta* reached exceptionally high values, whereas *D. modigliani* had disappeared.

The calanoid species, *Phyllodiaptomus annae* and *Heliodiaptomus viduus*, showed high daily production values (Figure 3). In contrast to the relatively high contribution of egg production to total production in cladocerans, in copepods egg production is relatively unimportant (compare Figures 2 and 4). For most copepod species, almost 50% of the production can be attributed to the naupliar stages (Figure 4). This is predominantly because of their relatively high productivity, mean naupliar P/B = 0.38 versus a mean P/B of 0.10 for the copepodite instars. Generally, the calanoids contribute more than the cyclopoids to the total copepod production. Although copepods generally showed a lower P/B than cladocerans (compare Figures 1 and 3), as a result of the generally higher biomass stock of the copepods, total copepod production was generally higher than cladoceran production in the course of the two years, except in December 1992, just after the drought, when *C. cornuta* was responsible for 80% of the total microcrustacean production. Annually, ca two-thirds of the

total microcrustacean production was realised by the copepods.

## Discussion

### *Length–weight relationships*

The variation among the length–weight regression lines, reported in the literature is high (Figure 5), which may be partly caused by temporal fluctuations in the condition (i.e. dry weight in relation to size) because of changes in the extent of food limitation. In microcrustaceans inhabiting the temperate regions, the seasonal variations in length-specific weight content may be high (e.g. Duncan, 1985; Boersma & Vijverberg, 1994b). The latter authors reported differences of a factor 3 for two *Daphnia* spp. and its hybrid in a eutrophic lake. Although the extent of the variation in the dry weight content of tropical crustaceans is not known the temporal changes in fecundity suggest that at least some seasonal changes in food availability do

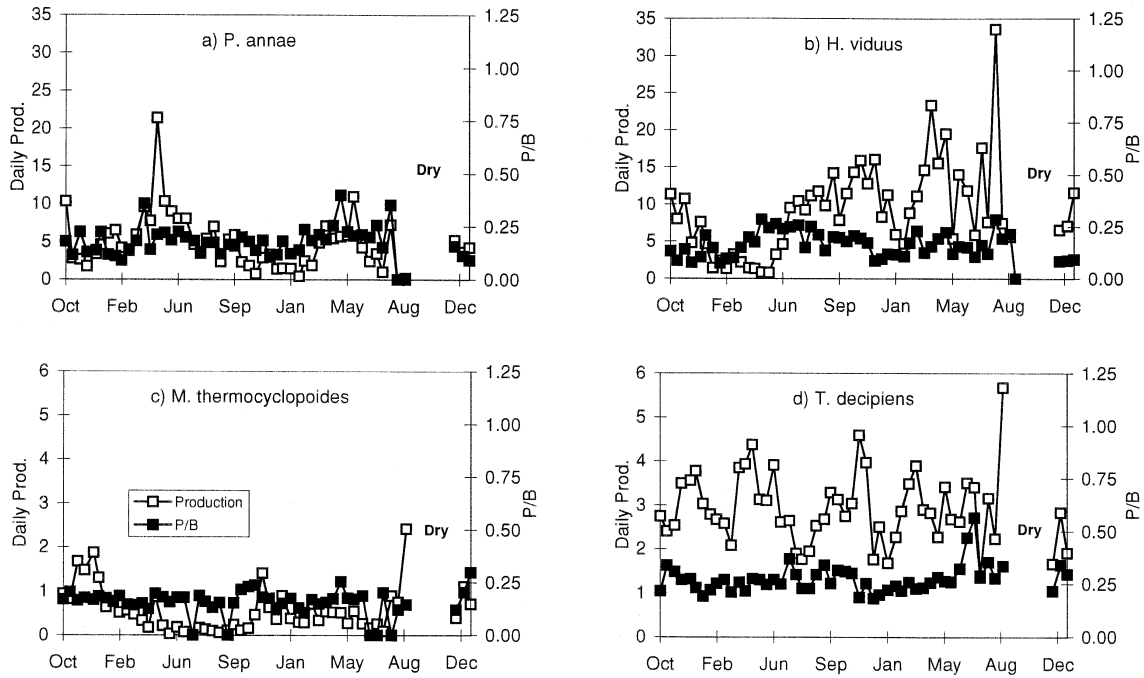


Figure 3. Daily production ( $\text{mg C l}^{-1} \text{d}^{-1}$ ) and daily P/B ratios of four copepod species in Tissawewa over the period October 1990 until December 1992: (a) *Phyllodiaptomus annae*, (b) *Heliodiaptomus viduus*, (c) *Mesocyclops thermocycloides*, (d) *Thermocyclops decipiens*. 'Dry' indicates drought period. Note the different scales for production.

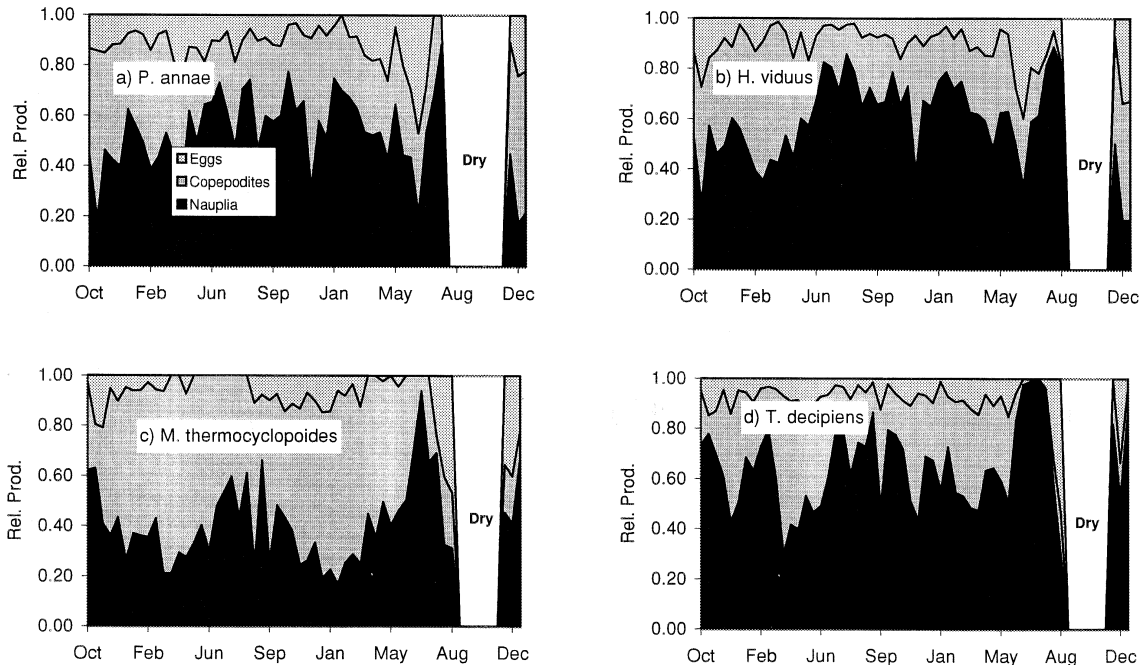


Figure 4. Relative contribution to the total production of nauplii, copepodites and eggs of (a) *P. annae*, (b) *H. viduus*, (c) *M. thermocycloides*, (d) *T. decipiens*, in Tissawewa over the period October 1990 until December 1992. 'Dry' indicates drought period.



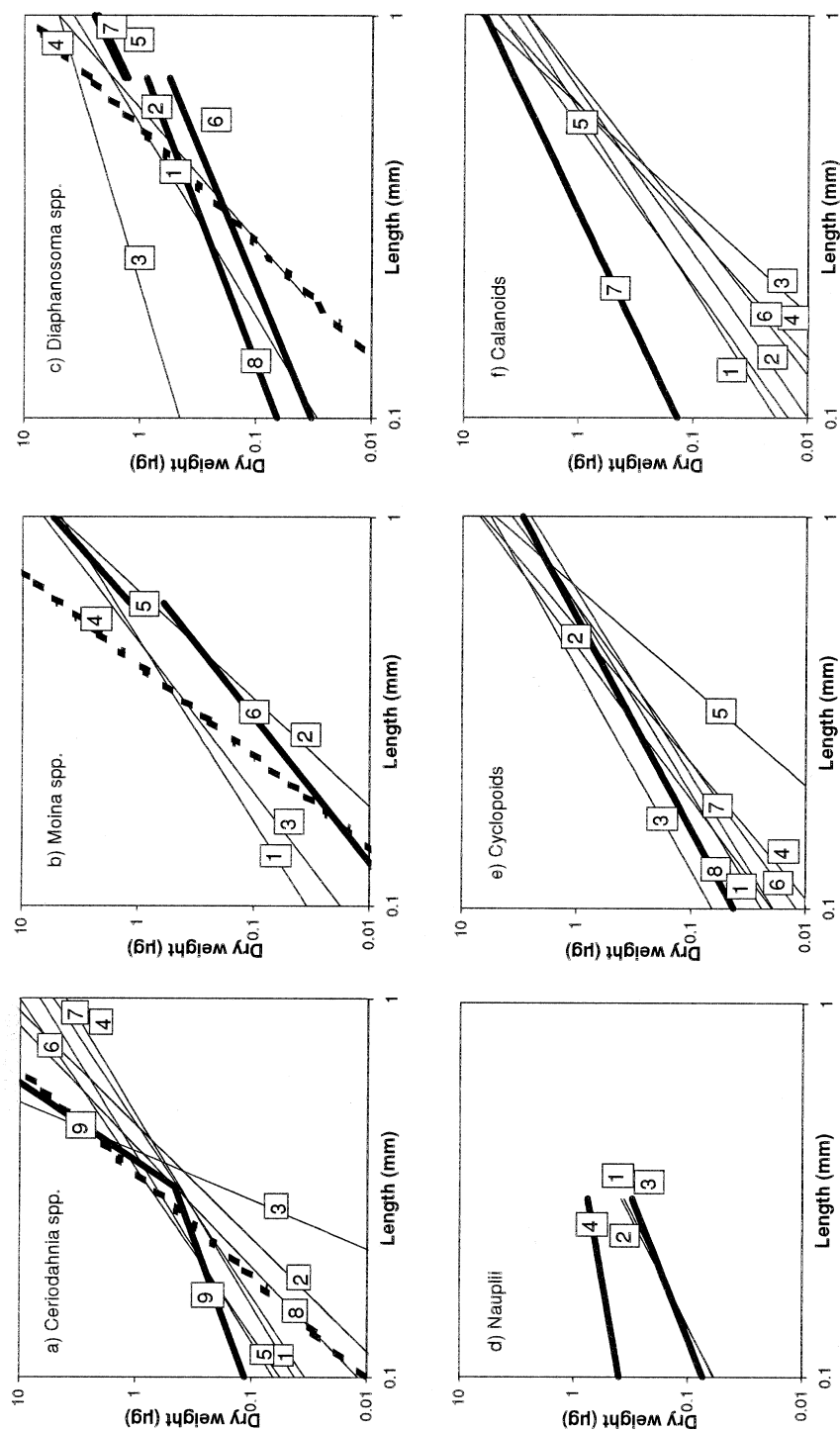


Figure 5. Length-weight relationships of several cladoceran and copepod taxa in relation to published values derived from the literature of (a) *Ceriodaphnia* spp., (b) *Moina* spp., (c) *Diaphanosoma* spp., (d) Nauplii, (e) Calanoid copepods, and (f) Cyclopoid copepods. Bold solid lines: This study, bold broken lines: Jayatunga & Duncan (1990), thin solid lines: all other studies. \* = non-preserved material or corrected for preservation effects. Authorities: (a) *Ceriodaphnia*: (1) *C. quadrangula* (Dumont et al., 1975), (2) *C. quadrangula* (Bottrell et al., 1976), (3) *C. quadrangula* (Rosen, 1981), (4) *C. lacustris*-without eggs (Culver et al., 1985), (5) *C. reticulata* (Dumont et al., 1975), (6) *C. reticulata*\* (Pace & Orcutt, 1981), (7) *C. cornuta* (Masundire, 1994), (8) *C. cornuta*\* (Jayatunga & Duncan, 1990), (9) *C. cornuta*\*-with eggs (This study), (10) *C. cornuta*\*-without eggs (This study); (b) *Moina*: (1) *M. mangolica*-juveniles (Dumont et al., 1975), (2) *M. mangolica*-adults (Dumont et al., 1975), (3) *M. micrura* (Dumont et al., 1975), (4) *M. micrura*\* (Jayatunga & Duncan, 1990), (5) *M. micrura*\*-with eggs (This study), (6) *M. micrura*\*-without eggs (This study); (c) *Diaphanosoma*: (1) *D. brachyurum* (Dumont et al., 1975), (2) *D. brachyurum* (Bottrell et al., 1975), (3) *D. leuchtenbergianum* (Culver et al., 1985), (4) *D. excisum*\* (Jayatunga & Duncan, 1990), (5) *D. modigliani*-with eggs (This study), (6) *D. modigliani*\*-without eggs (This study), (7) *D. excisum*\*-with eggs (This study), (8) *D. excisum*\*-without eggs (This study); (d) Nauplii: (1) cyclopoid nauplii (Culver et al., 1985), (2) calanoid nauplii (Culver et al., 1985), (3) cyclopoid nauplii\* (This study), (4) *Acanthocyclops robustus* (Pont, 1983), (2) *A. vernalis* (Culver et al., 1985), (3) *Cyclops bicuspidatus* (Culver et al., 1985), (4) *Mesocyclops edax* (Culver et al., 1985), (5) *M. edax* (Rosen, 1981), (6) *Thermocyclops hyalinus* (Burgis, 1974), (7) *Thermocyclops* sp. (Masundire, 1994), (8) *Mesocyclops thermocycloides* and *Thermocyclops decipiens*\* (This study); (f) Calanoids: (1) *Diaptomus gracilis* (Bottrell et al., 1975), (2) *D. siltoide*\* (Pace & Orcutt, 1981), (3) *Diaptomus* sp. (Culver et al., 1985), (4) *Eudiaptomus graciloides*\* (Persson & Ekbohm, 1980), (5) *E. gracilis*\* (Persson & Ekbohm, 1980), (6) *Tropadiaptomus* sp. (Masundire, 1994), (7) *Heliodiaptomus viduus* and *Phylloidiaptomus annae*\* (This study).

occur. Hence changes in the carbon contents are also to be expected.

Most length–weight relationships reported in the literature were derived from animals preserved in formalin, and this preservation method is known to cause losses in the carbon content of animals (e.g. Salonen & Sarvala, 1985). In this study we corrected for these losses, one would expect that the carbon content of the animals in our study to be higher. Of the published length–weight relationships relevant for this study only three out of the ten studies used non-preserved zooplankton (i.e. Persson & Ekbohm, 1980; Pace & Orcutt, 1981; Jayatunga & Duncan, 1990) (see legend Figure 5). The results of Jayatunga & Duncan (1990) are of special interest because they concern the same cladoceran species, and are from the same region (Sri Lanka), as the cladocerans of the present study. We compared the zooplankton length–weight relationships of the present study with those given in the literature, taxon by taxon (Figure 5). For *Ceriodaphnia* we conclude that the relationship we calculated for *C. cornuta* is similar to the relationships given in the literature, there is only one exception (Rosen, 1981). The relationship given by Jayatunga & Duncan (1990) is almost the same for what we observed for adults with eggs, but the juveniles differ. For *Moina* our observation for *M. micrura* falls in the same range as the results published in the literature, the slope of the regression line given by Jayatunga & Duncan (1990) seems steeper than our regression for the same species. For *Diaphanosoma* our observations for *D. modigliani* and *D. excisuma* agree well with most other observations, the results of Culver et al. (1985) for *D. leuchtenbergianum* are the only exception. The slope of the regression of Jayatunga & Duncan (1990) seems steeper than the slopes of the other regressions lines. For copepod nauplii our length–weight relationship for cyclopoid copepods is very similar to the relationship given by Culver et al. (1985) for the same taxon, but our length–weight relationship for calanoid nauplii is different. For cyclopoid copepodites our length–weight relationship for *Mesocyclops thermocyclopoides* and *Thermocyclops decipiens* is similar to what is reported in the literature, there is only one exception (Rosen, 1981). For calanoid copepodites our length–weight relationship is quite different from what was observed by others, since half of the published relationships were based on non-preserved copepods this is probably the result of the morphology of the two species used in the present study (*Heliodiaptomus viduus*, *Phyllodiaptomus annae*).

#### *Biomass, production, and P/B estimates for the zooplankton in Tissawewa*

Of the eight zooplankton species in Tissawewa six had an P/B ratio well above those predicted by Banse & Mosher (1980: Eqn 10) on the basis of body mass at maturity, whereas only two species (*Di. modigliani* and *M. thermocyclopoides*) had ratios which were similar to those predicted by the Banse and Mosher model. For the cladoceran species we found a good correspondence between log P/B and the log of average adult mass at maturity ( $r^2 = 0.91$ , slope =  $-1.01$ ,  $N = 4$ ), whilst this relationship was weak for the copepod species ( $r^2 = 0.29$ , slope =  $-0.12$ ,  $N = 4$ ). Banse and Mosher (1980) based their predictions on a regression model for which they used published data for invertebrates which were collected over a large geographical area, with an estimated mean temperature in the range of 5–20 °C. On basis of these data these authors failed to find a significant correlation between mass-scaled P/B and temperature. This is surprising because it is well known from the literature that under conditions of no, or only moderate food limitation size-specific growth rate and temperature are strongly positive related (e.g. Vijverberg, 1980). Since the annual temperature range in Tissawewa was 24.7–31.8 °C (Amarasinghe unpubl.), the higher P/B ratios observed in our study may well have been caused by the higher temperatures. The steep slope of the regression line between log P/B with the log body mass at maturity for the cladocerans in this study strongly suggests only a moderate food limitation of growth and production, this in contrast with the copepods for which the poor correspondence between P/B and adult mass at maturity indicates severe food limitation. In contrast with the present study, Saunders & Lewis (1988) observed for all zooplankton species in hypertrophic Lake Valencia P/B ratios well below those predicted by the Banse & Mosher (1980) equation. Furthermore, they found no correspondence between P/B and average adult mass at maturity, which suggest that these populations were all severely food limited.

The production of the microcrustacean community of the eutrophic Tissawewa was primarily due to two calanoid copepods, *Phyllodiaptomus annae* and *Heliodiaptomus viduus*. A zooplankton community permanently dominated by copepods, either cyclopoids or calanoids, is characteristic for almost all tropical and subtropical lakes and reservoirs (e.g. Burgis, 1974; Lewis, 1979; Leveque & Saint-Jean, 1983; Burgis, 1984; Vareschi & Vareschi, 1984; Hart, 1987;

Mengestou & Fernando, 1991, Mavuti, 1994). This is in contrast with what is generally known from eutrophic lakes and reservoirs in the northern temperate regions, which are generally dominated by cladocerans during the warmer period of the year and by cyclopoid copepods during the colder period of the year (see review by Morgan et al., 1980). A relatively high contribution of eggs to total net production for cladocerans (>60%) has been earlier reported by Vijverberg & Richter (1982a), Taylor (1985), Lynch (1989, 1992) and Anderson & Benke (1994) if food conditions are non-limiting, even in large-bodied *Daphnia* spp. gonad production will contribute >60% to total production, and smaller species tend to invest still more. In the small-bodied species, *Ceriodaphnia dubia*, cultured on natural seston, egg production measured over the entire lifespan accounted for 85-88% of the total production at water temperatures  $\geq 20$  °C (Anderson & Benke, 1994). The relative low contribution of egg production to total production in copepods is to be expected, as copepods in contrast to cladocerans reproduce only at the final adult size. Similar low proportion of egg production to total production for copepods in tropical lakes was reported by Lewis (1979) for Lake Lanao in Philippines, by Gras & Saint-Jean (1983) for Lake Chad, by Mengestou & Fernando (1991) for Lake Awasa in Ethiopia, and Vijverberg & Richter (1982b) observed similar low proportions for two cyclopoids in Tjeukemeer, a northern temperate lake. On the other hand Vareschi & Jacobs (1984) did report an exceptional high value (>50%) for the calanoid copepod *Paradiaptomus africana* in Lake Nakuru (Kenya). In our study the low contribution of egg production was compensated by the high (ca 40–70%) contribution of naupliar somatic production to the total copepod net production. This is high compared with the ca 30% contribution reported by Mengestou & Fernando (1991) for two cyclopoid copepod species in Lake Awasa, but very similar to the values observed by Vijverberg & Richter (1982b) for two cyclopoids in lake Tjeukemeer.

#### *Comparisons with 'other' tropical and subtropical lakes and reservoirs*

##### *Zooplankton biomass*

Based on the production ecology of microcrustacean zooplankton from more than twenty tropical and subtropical lakes and reservoirs of varying morphometry and trophy including our reservoirs (Tables 4 and 5), we investigated the relationship between phyto-

Table 4. Limnological classification of trophic status of lakes and reservoirs, slightly modified from Lee et al. (1981).

Classification	Average phytoplankton biomass (mg dry wt m <sup>-3</sup> )
Oligotrophic	<100
Oligotrophic-mesotrophic	100–149
Mesotrophic	150–349
Mesotrophic-eutrophic	350–499
Eutrophic	500–999
Hypertrophic	>1000

plankton biomass and zooplankton biomass and plotted regression relationships (Figure 6). We observed a strong positive (slope = 0.45;  $r^2 = 0.58$ ) and significant ( $P < 0.001$ ) relationship between phytoplankton biomass and microcrustacean zooplankton biomass (Table 6), as observed by several other authors for temperate lakes; McCauley & Kalff (1981) for seventeen northern temperate lakes; Mills & Schavione (1982) for thirteen New York lakes; Hanson & Peters (1984) for forty-seven northern temperate lakes and two African lakes; Rognerud & Kjelberg (1990) for eighteen Norwegian lakes; and Malthus & Mitchell (1990) for nineteen New Zealand lakes. In contrast, three studies failed to find a significant relationship or showed a weak correlation ( $P > 0.05$ ;  $r^2 < 0.2$ ) between phytoplankton biomass and microcrustacean biomass: Yan & Strus (1980) for twenty-one lakes in Ontario (Canada), Campbell & Knoechel (1988) for seventeen lakes on the Avalon Peninsula (New Foundland, Canada) and Bays & Crisman (1983) for thirty-nine subtropical lakes in Florida. Thus, such biomass comparisons of a wide range of lakes over large geographical areas, generally reveal significant and strong correlations, for both tropical lakes and reservoirs (this study) and temperate lakes and reservoirs (McCauley & Kalff, 1981; Hanson & Peters, 1984; Malthus & Mitchell, 1990). In contrast, regional models based on waterbodies in a restricted geographical region, with similar climatic, geological and biological conditions, often do not indicate such a relationship. These waterbodies are likely to show a narrower range of trophic conditions, and, therefore, differences in zooplankton biomass are probably affected less by the relative small disparities in resource availability, and more by differences in predation pressure exerted by fish or invertebrates, but effects of these factors are not included in the regression models employed in these studies.

*Table 5.* List of tropical lakes and reservoirs for which secondary production data were obtained with characteristics and authority. Trophic status is based upon the average phytoplankton biomass, according to the modified classification of Lee et al. (1981) (see Table 4). Abbreviations used: oligo=oligotrophic; om= oligotrophic-mesotrophic; meso=mesotrophic; me= mesotrophic-eutrophic; eu=eutrophic; hyper=hypertrophic. Generally, for depth the mean depth ( $Z_{\text{mean}}$ ) is given, when this information was not available the maximum depth is given instead ( $Z_{\text{max}}$ ; \*).

Waterbody	Latitude	Altitude (m)	Mean $Z$ (m)	Trophic status	Reference
1. Awasa	7° N		10.0	Hyper	Mengestou & Fernando (1991)
2. Chad	13° N	282	3.5	Hyper	Carmouze et al. (1983); Leveque & Saint-Jean (1983)
3. Cote d'Ivoire ponds	5° N		1.0	Hyper	Saint-Jean & Bonou (1994)
4. George	0° N/S	913	2.4	Hyper	Burgis (1974,1978)
5. Kariba	17° S		29	Oligo	Machena et al. (1993)
6. Kinneret	32° N		24	Meso	Walline et al. (1993)
7. Kenyir	5° N		36.9	Meso	Jamaludin (1993)
8. Lanao	8° N		60.3	Meso	Lewis (1979)
9. Le Roux	30° S		15.0	Meso	Hart (1987)
10. Luguna de Bay	15° N		2.8	Hyper	Delos Reyes (1993)
11. Malawi	12° S		290	Oligo	Degnbol (1993)
12. Muruthawela	6° N		9.1	Me	This study
13. Naivasha	1° S	1890	5.0	Hyper	Mavuti (1994)
14. Nakuru	0° N/S		2.3	Hyper	Vareschi & Jacobs (1984); Vareschi & Vareschi (1984)
15. Ridiyagama	6° N		3.0	Eu	This study
16. Sibaya	27° S		13	Meso	Hart & Allanson (1975); Allanson (1979)
17. Tanganyika	7° S		570	Oligo	Hecky (1984); Moreau et al. (1993b)
18. Tissawewa	6° N		1.7	Eu	This study
19. Titicaca	16° S	3800	280*	Oligo	Widmer et al. (1975)
20. Turkana	3° N		312	Oligo	Kolding (1993)
21. Vialencia	10° N		18	Hyper	Saunders & Lewis (1988)
22. Veli	8° N		2.0	Hyper	Aravindan (1993)
23. Victoria	0° S		93	Oligo	Moreau et al. (1993a)

*Table 6.* Model parameters for regression of  $\log_{10}$  transformed mean zooplankton biomass (Bzoopl), annual zooplankton production (Pzoopl), and untransformed daily P/B ratios for total zooplankton, large-bodied cladocerans, small-bodied cladocerans, and copepods as the dependent variables and  $\log_{10}$  mean phytoplankton biomass (Bphyto) as the independent variable.

Dependent variable ( $Y'$ )	Slope	Intercept	$r^2$	$P <$
Bzoopl	0.451	0.801	0.58	0.001
Pzoopl	0.447	2.396	0.43	0.001
P/Bzoopl	-2.721	55.33	0.02	0.14
P/B large-bodied cladocerans	0.132	-0.169	0.25	0.097
P/B small-bodied cladocerans	0.177	-0.118	0.19	0.15
P/B copepods	-0.032	0.237	0.12	0.11

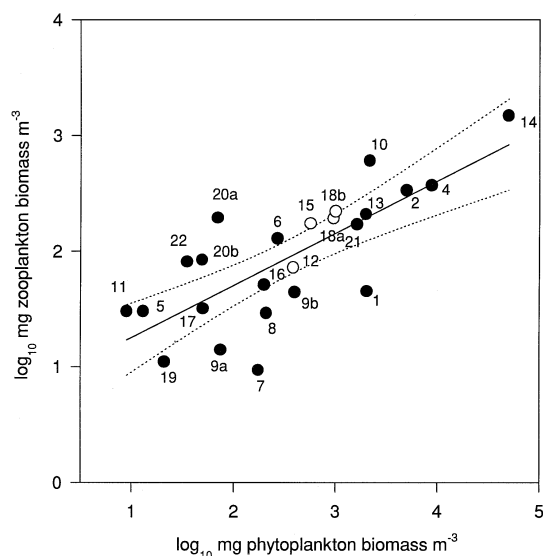


Figure 6. Relation between  $\log_{10}$  mean phytoplankton biomass ( $\text{mg dry wt m}^{-3}$ ) and  $\log_{10}$  mean zooplankton biomass ( $\text{mg dry wt m}^{-3}$ ) in tropical and subtropical lakes and reservoirs, showing the position of Muruthawela, Ridiyagama, and Tissawewa (open symbols) and the other lakes (closed symbols). The dotted lines are 95% confidence limits about predicted values outside the regression model. Numbers next to the data points refer to waterbodies, for name of waterbody and authority see Table 5. Observations on waterbodies in different years: 9a=Le Roux 1981–82; 9b=Le Roux 1982–83; 18a=Tissawewa 1990–91; 18b=Tissawewa 1991–92; 20a=Turkana 1973; 20b=Turkana 1987. For equation and summary statistics see Table 6.

The slope of the regression line which describes the relationship between mean phytoplankton biomass and mean zooplankton biomass for twenty-three tropical and subtropical lakes is significantly smaller than 1.0 ( $P < 0.05$ ) (Figure 6), which indicates that the ratio of zooplankton biomass to phytoplankton biomass decreases with increasing trophity. That is, as phytoplankton biomass increases, zooplankton biomass increases at a much smaller rate across the range of waterbodies examined. A similar trend was observed by McCauley & Kalff (1981) for seventeen northern-temperate lakes. Both observations are in agreement with the hypothesis formulated by Hillbricht-Ilkowska et al. (1972) which suggested that ecological transfer efficiency from phytoplankton towards microcrustacean zooplankton decreases with increasing trophity as the consequence of the increasing proportion of large and inedible algae in the more eutrophic waters. Gulati et al. (1985) who compared the relative assimilation rates of zooplankton with the seston concentrations for six lakes in The Netherlands also observed a signifi-

cant decrease in food utilization rates with increasing seston concentrations.

#### Zooplankton production

The correlation between mean phytoplankton biomass and mean zooplankton production is highly significant ( $P < 0.001$ ) and the correlation ( $r^2 = 0.43$ ) explains a fair amount of the observed variation in zooplankton production (Table 6). A positive relationship is expected since almost all zooplankton organisms included in this study are herbivorous, excepting the advanced copepodite instars of the less abundant cyclopoids (*M. thermocyclopoides* and *T. decipiens*). The exact feeding behaviour of the cyclopoid copepods in our study is not known but, based on what is known about the diets of other cyclopoid copepods, the advanced copepodite instars of these species are probably either carnivorous or omnivorous (Toth & Zankai, 1985; Irvine & Waya, 1993; Santer, 1993). Taking into consideration the trophic status of the reservoirs studied (i.e. eutrophic and mesotrophic), total zooplankton production is relatively high compared with the other tropical and subtropical waterbodies (Figure 7). For Muruthawela we might have overestimated the zooplankton production because we applied growth and development rates based on laboratory cultures, which had food concentrations which ca 3 times higher than in the reservoir. However, in general, when production values are compared over a large geographical area, mean phytoplankton biomass is a moderately good predictor of the total microcrustacean zooplankton production, explaining 43% of the observed variance.

#### P/B ratios

The zooplankton production per unit of biomass was not significantly related to the mean phytoplankton biomass. This seems surprising since both zooplankton production and zooplankton biomass are significantly related to phytoplankton biomass. Nevertheless, P/B of the herbivorous zooplankton will depend not only on concentration of the resource (phytoplankton) but also on the quality of the resource. The latter generally decreases with increase in resource concentration (Hillbricht-Ilkowska et al., 1972; Gulati et al., 1985), but is probably also highly variable among lakes with similar phytoplankton biomass because it will depend on the species composition of the phytoplankton present that in turn depends on a number of biotic and abiotic factors. The mean P/B ratios for the three categories were, as expected, high for the small-

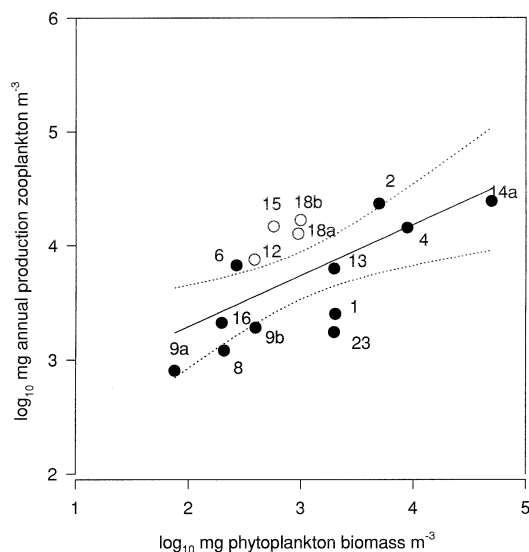


Figure 7. Relation between  $\log_{10}$  mean phytoplankton biomass ( $\text{mg dry wt m}^{-3}$ ) and  $\log_{10}$  annual zooplankton production ( $\text{mg dry wt m}^{-3} \text{ yr}^{-1}$ ) in tropical and subtropical lakes and reservoirs, showing the position of Muruthawela, Ridiyagama, and Tissawewa (open symbols) and the other lakes (closed symbols). The dotted lines are 95% confidence limits about predicted values outside the regression model. Numbers next to the data points refer to waterbodies, for name of waterbody and authority see Table 5. Observations on waterbodies in different years: 9a = Le Roux 1981–82; 9b = Le Roux 1982–83; 18a = Tissawewa 1990–91; 18b = Tissawewa 1991–92. For equation and summary statistics see Table 6.

bodied cladocerans (mean 0.41; range 0.12–0.95) (Figure 8), intermediate for the large-bodied cladocerans (mean 0.21; range 0.05–0.62) (Figure 9), and relatively low for the copepods (mean 0.14; 0.03–0.30) (Figure 10), but the variation within each category was very high. This is probably caused by the varying food conditions in the waterbodies where these species live. The P/B ratios for the cladoceran and copepod species of Tissawewa reservoir are generally well within the literature range for tropical and subtropical lakes and reservoirs. Only in three occasions fell the observed ratios outside the usual range. This was the case for the two copepod species, *T. decipiens* (both years), and *P. annae* (second year), which both showed relative high P/B values.

#### General conclusions

In the three Sri Lankan reservoirs studied the microcrustacean zooplankton biomass and production relative to the phytoplankton biomass present is relatively high, especially for the copepods. Both zooplank-

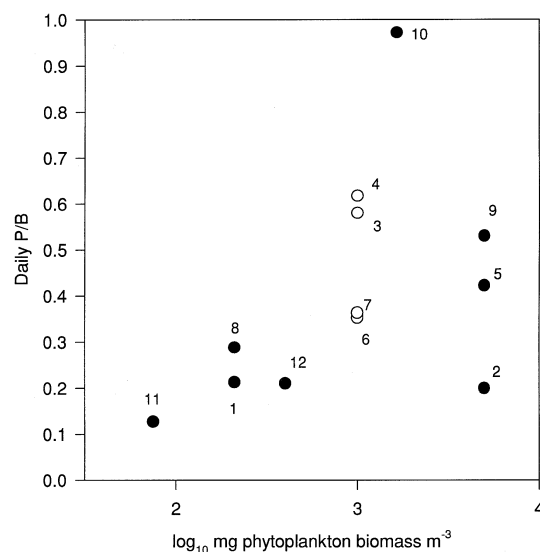


Figure 8. Relation between  $\log_{10}$  mean phytoplankton biomass ( $\text{mg dry wt m}^{-3}$ ) and the daily P/B of small-bodied (max. length ca 1.0 mm) cladoceran spp. in tropical and subtropical lakes and reservoirs, showing the position of Tissawewa (open symbols) and the other lakes (closed symbols). For authorities see Table 5, numbers next to the data points refer to species and waterbody: 1. *Bosmina fontalis* (Lanao); 2. *B. longirostris* (Chad); 3. *Ceriodaphnia cornuta* (Tissawewa 1990–91); 4. *C. cornuta* (Tissawewa 1991); 5. *C. cornuta* (Chad); 6. *Moina micrura* (Tissawewa 1990–91); 7. *M. micrura* (Tissawewa 1991–92); 8. *M. micrura* (Lanao); 9. *M. micrura* (Chad); 10. *M. micrura* (Côte d'Ivoire pond); 11. *M. brachiata* (Le Roux 1981–82); 12. *M. brachiata* (Le Roux 1982–83).

ton biomass and zooplankton production are positively related to phytoplankton biomass in twenty-two tropical lakes and reservoirs, mean phytoplankton biomass was a good predictor of mean zooplankton biomass and a moderate good predictor for annual zooplankton production. That a significant positive relationship was found is not surprising since there is a functional relationship between phytoplankton and zooplankton, however, the relatively high proportion of variance explained by the regression lines (58% and 43%) was not expected. The establishment of such relationships no doubt is a step forward in the better understanding of the dynamics of pelagic food webs in general but especially in the tropical region. Biomass size distributions provide a useful tool for ecosystem and community analysis owing to tight relationships between an individual's body mass, ensuing metabolic pathways (e.g. somatic growth rate, reproductive output, ingestion rate) and related ecological processes (e.g. success of predator avoidance) (Sprules et al., 1991). Therefore, the next step will be to compare zooplankton in tropics

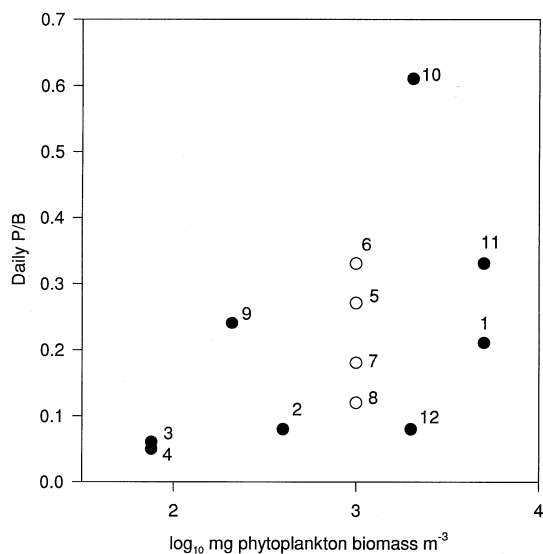


Figure 9. Relation between  $\log_{10}$  mean phytoplankton biomass ( $\text{mg dry wt m}^{-3}$ ) and the daily P/B of large-bodied (max. length  $>1.0$  mm) cladoceran spp. in tropical and subtropical lakes and reservoirs, showing the position of Tissawewa (open symbols) and the other lakes (closed symbols). For authorities see Table 5, numbers next to the data points refer to species and waterbody: 1. *Daphnia barbarata* and *D. lumholtzi* (Chad); 2. *D. barbarata* (Le Roux 1982-83); 3. *D. gibba* (Le Roux 1981-82); 4. *D. gibba* (Le Roux 1981-82); 5. *Diaphanosoma excisum* (Tissawewa 1990-91); 6. *Dia. excisum* (Tissawewa (1991-92)); 7. *Dia. modigliani* (Tissawewa 1990-91); 8. *Dia. modigliani* (Tissawewa 1991-92); 9. *Dia. modigliani* (Lanao); 10. *Dia. excisum* (Awasa); 11. *Dia. excisum* (Chad); 12. *Dia. excisum* (Naivasha).

versus temperate region, and the inclusion of body-size spectra in the predictive models.

## Acknowledgments

This study is the outcome of an international co-operation programme among the Departments of Zoology of the Ruhuna University (RU) at Matara (Sri Lanka), and the University of Leiden (The Netherlands) and The Netherlands Institute of Ecology – Centre for Limnology (CL) at Nieuwersluis (The Netherlands). The project was supported by grant RUL-40 from the Office of Foreign Cooperation of the University of Leiden. We thank our colleagues, Mr K. A. D. W. Senaratne (RU), Dr R. D. Gulati (CL), Dr H. J. Laanbroek (CL), Dr W. M. Mooij (CL), Mr G. J. Piet (CL), and Mr W. L. T. van Densen (Wageningen Agricultural University) for critically reviewing the manuscript. The reviewer Dr A. Dun-

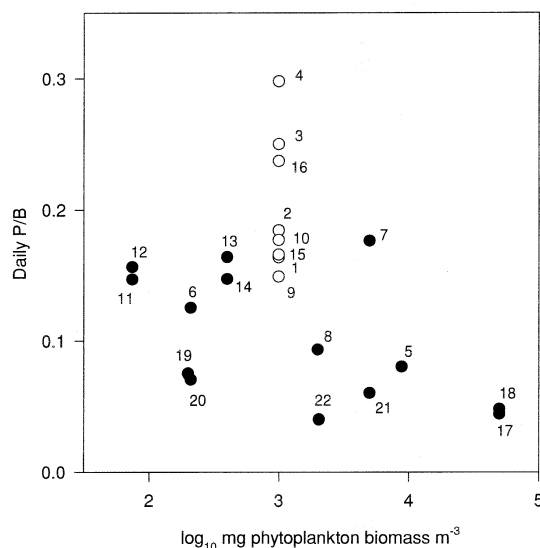


Figure 10. Relation between  $\log_{10}$  mean phytoplankton biomass ( $\text{mg dry wt m}^{-3}$ ) and the daily P/B of copepod spp. in tropical and subtropical lakes and reservoirs, showing the position of Tissawewa (open symbols) and other lakes (closed symbols). For authorities see Table 5, numbers next to the data points refer to species and waterbody: 1. *Mesocyclops thermocyclopides* (Tissawewa 1990-91); 2. *M. thermocyclopides* (Tissawewa 1991-92); 3. *Thermocyclops decipiens* (Tissawewa 1990-91); 4. *Th. decipiens* (Tissawewa 1991-92); 5. *Th. hyalinus* (George); 6. *Th. hyalinus* (Lanao); 7. *Th. neglectes* (Chad); 8. *Th. oblongatus* (Naivasha); 9. *Heliodiaptomus viduus* (Tissawewa 1990-91); 10. *H. viduus* (Tissawewa 1991-92); 11. *Lovenula excellens* (Le Roux 1981-82); 12. *L. excellens* (Le Roux (1982-83)); 13. *Metadiaptomus meridianus* (Le Roux 1981-82); 14. *M. meridianus* (Le Roux 1982-83); 15. *Phyllodiaptomus annae* (Tissawewa 1990-91); 16. *P. annae* (Tissawewa 1991-92); 17. *Paradiaptomus africana* (Nakuru 1972); 18. *P. africana* (Nakuru 1973); 19. *Pseudodiaptomus hessei* (Sibaya); 20. *Tropodiaptomus gigantoviger* (Lanao); 21. *T. incognitus* (Chad); 22. *Mesocyclops aequatorialis* (Awasa).

can is acknowledged for her critical comments on the manuscript. We thank Dr P. R. T. Cumararatunga (RU) for helpful suggestions, and the research assistants Mr J. P. L. Hettige, and Mr R. A. Maitheepala for their assistance in the field and for their help with the analysis of the field samples, and Mr G. Postema for the improvements of the graphs.

## References

- Allanson, B. R., 1979. Lake Sibaya. Monographiae Biologicae Vol. 36. Dr W. Junk Publishers, The Hague, 364 pp.
- Amarasinghe, P. B., M. Boersma & J. Vijverberg, 1997. The effect of temperature, and food quantity and quality on the growth and development rates in laboratory-cultured copepods and cladocerans from a Sri Lankan reservoir. *Hydrobiologia*, 350: 131-144.

- Anderson, D. H. & A. C. Benke, 1994. Growth and reproduction of the cladoceran *Ceriodaphnia dubia* from a forested floodplain swamp. *Limnol. Oceanogr.* 39: 1517–1527.
- Aravindan, C. M., 1993. Preliminary trophic model of Veli Lake, Southern India. In Christensen, V. & D. Pauly (eds), *Trophic Models of Aquatic Ecosystems*, ICLARM, Manila, Philippines: 87–89.
- Bailey-Watts, A. E., 1974. The algal plankton of Loch Leven, Kinross. *Proc. r. Soc. Edinb. (B)* 74: 135–156.
- Banase, K. & S. Mosher, 1980. Adult body mass and annual production/biomass relationships of field populations. *Ecol. Monogr.* 50: 355–379.
- Bays, J. S. & T. L. Crisman, 1983. Zooplankton and trophic state relationships in Florida lakes. *Can. J. Fish. aquat. Sci.* 40: 1813–1819.
- Benke, A. C., 1993. Edgardo Baldi Memorial Lecture: Concepts and patterns of invertebrate production in running waters. *Verh. int. Ver. Limnol.* 25: 15–38.
- Boersma, M. & J. Vijverberg, 1994a. The effect of preservation methods on the carbon content of *Daphnia*. *Arch. Hydrobiol.* 130: 241–247.
- Boersma, M. & J. Vijverberg, 1994b. Seasonal variations in condition of two *Daphnia* species and their hybrid in a eutrophic lake: evidence for food limitation under field conditions. *J. Plankton Res.* 16: 1793–1809.
- Bottrell, H. H., A. Duncan, Z. M. Gliwicz, E. Grygierek, A. Herzig, A. Hillbricht-Ilkowska, H. Kurasawa, P. Larsson & T. Weglenska, 1976. A review of some problems in zooplankton production studies. *Norw. J. Zool.* 24: 419–456.
- Burgis, M. J., 1974. Revised estimates for the biomass and production of zooplankton in Lake George, Uganda. *Freshwat. Biol.* 4: 535–541.
- Burgis, M. J., 1978. Case studies of lake ecosystems at different latitudes: The tropics. The Lake George ecosystems. *Verh. int. Ver. Limnol.* 20: 1139–1152.
- Campbell, C. E. & R. Knoechel, 1988. Zooplankton communities and trophic structure of lakes on the Avalon Peninsula, Newfoundland, Canada. *Verh. int. Ver. Limnol.* 23: 297–305.
- Carmouze, J. P., J. R. Durand & C. L  veque, 1983. Lake Chad – Ecology and Productivity of a Shallow Tropical Ecosystem. *Monographiae Biologicae* 53, Dr W. Junk Publishers, The Hague.
- Culver, D. A., M. M. Boucherle, D. J. Bean & J. W. Fletcher, 1985. Biomass of freshwater crustacean zooplankton from length–weight regressions. *Can. J. Fish. aquat. Sci.* 42: 1380–1390.
- Degnbol, P., 1993. The pelagic zone of central Lake Malawi – A trophic box model. In Christensen, V. & D. Pauly (eds), *Trophic Models of Aquatic Ecosystems*, ICLARM, Manila, Philippines: 110–115.
- Delos Reyes, M. R., 1993. Fishpen culture and its impact on the ecosystem of Laguna de Bay, Philippines. In Christensen, V. & D. Pauly (eds), *Trophic Models of Aquatic Ecosystems*, ICLARM, Manila, Philippines: 74–84.
- Dumont, H. J., I. Van de Velde & S. Dumont, 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from plankton periphyton and benthos of continental waters. *Oecologia* 19: 75–97.
- Duncan, A., 1985. Body carbon in daphnids as an indicator of the food concentrations available in the field. *Arch. Hydrobiol. Beih.* 21: 81–90.
- Fernando, C. H., 1980. The species and size composition of tropical freshwater zooplankton with special reference to the Oriental region (South East Asia). *Int. Revue ges. Hydrobiol.* 65: 411–426.
- Gras, R. & L. Saint-Jean, 1983. Production du zooplankton du Lac Tchad. *Revue Hydrobiol. trop.* 16: 57–77.
- Gulati, R. D., K. Siewertsen & G. Postema, 1985. Zooplankton structure and grazing activities in relation to food quality and concentration in Dutch lakes. *Arch. Hydrobiol. Beih.* 21: 91–102.
- Hanson, J. M. & R. H. Peters, 1984. Empirical prediction of crustacean zooplankton biomass and profundal macrobenthos biomass in lakes. *Can. J. Fish. aquat. Sci.* 41: 439–445.
- Hart, R. C., 1987. Population dynamics and reproduction of five crustacean zooplankters in a subtropical reservoir during years of contrasting turbidity. *Freshwat. Biol.* 18: 287–318.
- Hart, R. C. & B. R. Allanson, 1975. Preliminary estimates of production by a calanoid copepod in subtropical Lake Sibaya. *Verh. int. Ver. Limnol.* 19: 1434–1441.
- Hecky, R. E., 1984. African lakes and their trophic efficiencies: a temporal perspective. In Meyers, D. G., J. R. Strickler. *Am. Assoc. Adv. Sci.*, Westview, Boulder: 405–448.
- Hillbricht-Ilkowska, A., I. Spondniewska, T. Weglenska & A. Karabin, 1972. The seasonal variation of some ecological efficiencies and production rates in the plankton community of several Polish lakes of different trophy. In Kajak, Z. & A. Hillbricht-Ilkowska (eds), *Productivity Problems of Freshwaters*, PWN Warszawa-Krakow: 111–127.
- Irvine, K. & R. Waya, 1993. Predatory behaviour of the cyclopoid copepod *Mesocyclops aequatorialis aequatorialis* in Lake Malawi, a deep tropical lake. *Verh. int. Ver. Limnol.* 25: 877–881.
- Jamaludin, B. I., 1993. Spatial and temporal patterns in the zooplankton in Senenyih and Kenyir reservoir Malaysia and an estimation of zooplankton production. M.Sc. Thesis Wageningen Agricultural University, The Netherlands, 66 pp.
- Jayatunga, Y. N. A. & A. Duncan, 1990. Body carbon weight–length relationship for four tropical cladoceran species grown under well defined food level and temperature. *Ceylon J. Sci. (Bio. Sci.)* 21: 34–40.
- Kolding, J., 1993. Trophic interrelationships and community structure at two different periods of Lake Turkana, Kenya: a comparison using the ECOPATH II box model. In Christensen, V. & D. Pauly (eds), *Trophic Models of Aquatic Ecosystems*, ICLARM, Manila, Philippines: 116–123.
- Lee, F. G., R. A. Jones & W. Rast, 1981. Alternative approach to trophic state classification for water quality management. International Joint Commission, Washington, D.C., Department of Civil Engineering, Occasional Paper 66: 5–65.
- L  v  que, C. & L. Saint-Jean, 1983. Secondary production (zooplankton and benthos). In Carmouze, J. P., J. R. Durand & C. L  v  que (eds), *Lake Chad – Ecology and Productivity of a Shallow Tropical Ecosystem*, Dr W. Junk Publishers, The Hague: 385–424.
- Lewis, W. M. Jr., 1979. Zooplankton Community Analysis: Studies on a Tropical System. Springer-Verlag, New York, Heidelberg, Berlin, 163 pp.
- Lewis, W. M. Jr., 1987. Tropical limnology. *Ann. Rev. Ecol. Syst.* 18: 159–184.
- Lynch, M., 1989. The life history consequences of resource depression in *Daphnia pulex*. *Ecology* 70: 246–256.
- Lynch, M., 1992. The life history consequences of resource depression in *Ceriodaphnia quadrangula* and *Daphnia ambigua*. *Ecology* 73: 1620–1629.
- Machena, C., J. Kolding & R. A. Sanyanga, 1993. A preliminary assessment of the trophic structure of Lake Kariba, Africa. In Christensen, V. & D. Pauly (eds), *Trophic Models of Aquatic Ecosystems*: 130–137.



- Malthus, T. J. & S. F. Mitchell, 1990. On the occurrence, causes and potential consequences of low zooplankton to phytoplankton ratios in New Zealand lakes. *Freshwat. Biol.* 22: 383–394.
- Masundire, H. M., 1994. Mean individual dry weight and length-weight regressions of some zooplankton of Lake Kariba. *Hydrobiologia* 272: 231–238.
- Mavuti, K. M., 1994. Durations of development and production estimates by two crustacean zooplankton species *Thermocyclops oblongatus* Sars (Copepoda) and *Diaphanosoma excisum* Sars (Cladocera), in Lake Naivasha, Kenya. *Hydrobiologia* 272: 185–200.
- McCaughey, E. & J. Kalf, 1981. Empirical relationships between phytoplankton and zooplankton biomass in lakes. *Can. J. Fish. aquat. Sci.* 38: 458–463.
- Mengestou, S. & C. H. Fernando, 1991. Biomass and production of the major dominant crustacean zooplankton in a tropical Rift Valley lake, Awasa, Ethiopia. *J. Plankton Res.* 13: 831–851.
- Mills, E. L. & A. Schavone Jr., 1982. Evaluation of fish communities through assessment of zooplankton populations and measures of lake productivity. *N. Am. J. Fish. Mgmt* 2: 14–27.
- Moreau, J., W. Ligtvoet & M. L. D. Palomares, 1993a. Trophic relationship in the fish community of Lake Victoria, Kenya, with emphasis on the impact of Nile perch (*Lates niloticus*). In Christensen, V. & D. Pauly (eds), *Trophic Models of Aquatic Ecosystems*, 144–152.
- Moreau, J., B. Nyakageni, M. Pearce & P. Petit, 1993b. Trophic relationships in the pelagic zone of Lake Tanganyika (Burundi sector). In Christensen, V. & D. Pauly (eds), *Trophic Models of Aquatic Ecosystems*. ICLARM, Manila, Philippines: 138–143.
- Morgan, N. C., T. Backiel, G. Bretschko, A. Duncan, A. Hillbricht-Ilkowska, Z. Kajak, J. F. Kitchell, P. Larsson, C. Leveque, A. Nauwerck, F. Schiemer & J. E. Thorpe, 1980. Secondary production. In Le Cren, E. D. & R. H. Lowe-McConnell (eds), *The Functioning of Freshwater Ecosystems*. Cambridge University Press: 247–340.
- Omori, M., 1978. Some factors affecting on dry weight, organic weight and concentration of carbon and nitrogen in freshly prepared and in preserved zooplankton. *Int. Rev. Gesamt. Hydrobiol.* 63: 261–269.
- Pace, M. L. & J. D. Orcutt, Jr., 1981. The relative importance of protozoans, rotifers and crustaceans in a freshwater community. *Limnol. Oceanogr.* 26: 822–830.
- Persson, G. & G. Ekbohm, 1980. Estimation of dry weight in zooplankton populations: Methods applied to crustacean populations from lakes in the Kuokkel Area, Northern Sweden. *Arch. Hydrobiol.* 89: 225–246.
- Piet, G. J., J. Vijverberg & W. L. T. van Densen, in press. Food web structure of a Sri Lanka reservoir. In van Densen, W. L. T. & R. H. Lowe-McConnell (eds), *Lacustrine Fish Communities in S.E. Asia and Africa, Ecology and Exploitation*. Samarar Publishing Limited, Tresaith, UK.
- Plante, C. & J. A. Downing, 1989. Production of freshwater invertebrate populations in lakes. *Can. J. Fish. aquat. Sci.* 46: 1489–1498.
- Pont, D., 1983. Recherches quantitatives sur le peuplement de copépodes, cladocères et ostracodes des rizières de Camargue. Ph.D. thesis Faculté St. Charles Université de Provence Aix, Marseille.
- Riemann, B., P. Simonsen & L. Stensgaard, 1989. The carbon chlorophyll content of phytoplankton from various nutrient regimes. *J. Plankton Res.* 11: 1037–1045.
- Rigler, F. H. & J. A. Downing, 1984. The calculation of secondary productivity. In Downing, J. A. & F. H. Rigler (eds), *A Manual on Methods for the Assessment of Secondary Productivity in Fresh Waters*, chapter 2. IBP Hand Book no. 17, Black. Sci. Publ., London, 501 pp.
- Roff, J. C. & M. J. Tremblay, 1984. Singular, mass-specific P/B ratios cannot be used to estimate copepod production. Reply with additional notes on P/B ratios. *Can. J. Fish. aquat. Sci.* 41: 8320–8330.
- Rognerud, S. & G. Kjellberg, 1990. Long-term dynamics of the zooplankton community in Lake Mjfsa, the largest lake in Norway. *Verh. int. Ver. Limnol.* 24: 580–585.
- Rosen, R. A., 1981. Length-dry weight relationships of some freshwater zooplankton. *J. Freshwat. Ecol.* 1: 225–229.
- Saint-Jean, L. & C. A. Bonou, 1994. Growth, production, and demography of *Moina micrura* in brackish tropical fishponds (Layo, Ivory Coast). *Hydrobiologia* 272: 125–146.
- Salonen, K., 1979. A versatile method for the rapid and accurate determination of carbon by high temperature combustion. *Limnol. Oceanogr.* 24: 177–183.
- Salonen, K. & J. Sarvala, 1985. Combination of freezing and formaldehyde fixation, a superior preservation method for biomass determination of aquatic invertebrates. *Archiv fur Hydrobiologie* 103: 217–230.
- Santer, B., 1993. Potential importance of algae in the diet of adult *Cyclops vicinus*. *Freshwat. Biol.* 30: 269–278.
- Saunders, J. F. & W. M. Lewis Jr., 1988. Dynamics and control mechanisms in a tropical zooplankton community (Lake Valencia, Venezuela). *Ecol. Monogr.* 58: 337–353.
- Schram, M. D., G. R. Ploskey & E. H. Schmitz, 1981. Dry weight loss in *Ceriodaphnia* loss in *Ceriodaphnia lacustris* following formalin preservation. *Trans. am. Microsc. Soc.* 100: 326–329.
- Sokal, R. R. & F. J. Rohlf, 1995. *Biometry, the principles and practice of statistics in biological research* (3rd edn). Freeman Company, New York, 887 pp.
- Sprules, W. G., S. B. Brandt, D. J. Stewart, M. Munawar, E. H. Jin & J. Love, 1991. Biomass size spectrum of the Lake Michigan pelagic food web. *Can. J. Fish. aquat. Sci.* 48: 105–115.
- Statsoft, 1992. *CSS: Statistica. Volume I, Conventions and statistics I*. Statsoft Inc., Tulsa, Oklahoma, 679 pp.
- Tóth, L. G. & N. P. Zankai, 1985. Feeding of *Cyclops vicinus* (Uljanin) (Copepoda: Cyclopoida) in Lake Balaton on the basis of gut content analyses. *Hydrobiologia* 122: 251–260.
- Vareschi, E. & J. Jacobs, 1984. The ecology of lake Nakuru (Kenya). V. Production and consumption of consumer organisms. *Oecologia* 61: 83–98.
- Vareschi, E. & A. Vareschi, 1984. The ecology of Lake Nakuru (Kenya). IV. Biomass and distribution of consumer organisms. *Oecologia* 61: 70–82.
- Vijverberg, J., 1980. Effect of temperature in laboratory studies on development and growth of Cladocera and Copepoda from Tjeukemeer, The Netherlands. *Freshwat. Biol.* 10: 317–340.
- Vijverberg, J., 1989. Culture techniques for studies on the growth, development and reproduction of copepods and cladocerans under laboratory and in situ conditions: a review. *Freshwat. Biol.* 21: 317–373.
- Vijverberg, J. & A. F. Richter, 1982a. Population dynamics and production of *Daphnia hyalina* Leydig and *Daphnia cucullata* Sars in Tjeukemeer. *Hydrobiologia* 95: 235–259.
- Vijverberg, J. & A. F. Richter, 1982b. Population dynamics and production of *Acanthocyclops robustus* (Sars) and *Mesocyclops leuckarti* (Claus) in Tjeukemeer. *Hydrobiologia* 95: 261–274.
- Walline, P. D., S. Pisanty, M. Gophen & T. Berman, 1993. The ecosystem of Lake Kinneret, Israel. In Christensen, V. & D. Pauly (eds), *Trophic models of aquatic ecosystems*. ICLARM, Manila, Philippines: 103–109.

- Widmer, C., T. Kitter & P. J. Richardson, 1975. A survey of the biological limnology of Lake Titicaca. *Verh. int. Ver. Limnol.* 19: 1504–1510.
- Winberg, G. G., K. Patalas, J. C. Wright, A. Hillbricht-Ilkowska, W. E. Cooper & K. H. Mann, 1971a. Methods for calculating productivity. In Edmondson, W. T. & G. G. Winberg (eds), *A Manual on Methods for the Assessment of Secondary Productivity in Fresh Waters*, Chapter 7, 296–317. IBP Handbook No. 17. Blackwell Scientific Publ., Edinburgh, 358 pp.
- Winberg, G. G., et al., 1971b. Symbols, units and conversion factors in studies of freshwater productivity. IBP Central Office London, 23 pp.
- Yan, N. D. & R. Strus, 1980. Crustacean zooplankton communities of acidic, metal-contaminated lakes near Sudbury, Ontario. *Can. J. Fish. aquat. Sci.* 37: 2282–229.