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The Dry Weight Estimate of Biomass in a Selection of Cladocera, Copepoda and Rotifera from the Plankton, Periphyton and Benthos of Continental Waters

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Summary. A procedure for determining dry weights has been standardized and applied to a number of Cladocera, Copepoda and Rotatoria. In most of the Cladocera, regression equations of the exponential type, relating dry weight to body length, were computed. In the Copepoda, one equation per suborder was computed, and suggestions for future refinements are made. In both groups, a fairly satisfactory agreement was found with literature data where these exist. In both groups, the egg and embryo weight proved to be considerable, relative to the weight of the adult female. In Rotatoria, 4 species could be dealt with in size-classes, and their weight increment per unit length was found to be lower than in the Cladocera and Copepoda. A large number of species were weighed as adults only. A conclusion applicable to the 3 groups is that, as a rule, limnetic species weigh relatively less than littoral, periphytic or benthic species. Even within a species, populations with a more pronounced limnetic way of life weigh less than populations of littoral nature.

Introduction

The study of food-chains, through which matter and energy flow, requires accurate assessments of one or both variables in respective gravimetric or energetic units. Although compartmentalized ecosystem models require consistent units of energy or biomass, less theoretical research in aquatic ecology also benefits from precise quantitative estimates of their variables. This statement may seem self-evident, but standing crops and production are too frequently expressed in terms of numbers of organisms per unit of volume or surface area. The value of such counts as estimates of matter or energy flow is conjectural. Although possibly neither the only nor the best of possible estimates, our choice of dry weight as a measure of biomass is adequate for a variety of applications.

In studies of aquatic micrometazoa, such dry weight data are rarely available. Until the recent development of microbalances made it possible to make routine weighings to 10^{-7} g, their determination was a heroic performance. Yet, Berg (1936) succeeded in weighing large-instar *Daphnia* with a precision remarkable for that time. An often-used approach in recent years was based on Lohmann's (1908) method, consisting of the determination of the mean volume of a species. Fresh weight computation assumed a density of 1.0 (*i.e.* $10^6\,\mu^3 = 1\,\mu g$). This approach is straightforward only for animals with simple geometry. In irregularly-shaped species, indirect techniques were used. Some calculated total volume by reducing it to a number of simple geometric shapes whose volumes are summed at the end (Osmera, 1966).

Others have constructed scale models of organisms and determine fresh weight by direct weighing or by measuring water displacement (Sebestyen, 1955, 1958a, b; Nauwerck, 1963). These procedures often involve an accumulation of errors. A better procedure has been widely used by some eastern European workers, where direct measurement of volume (wet weight) of various Cladocera and Copepoda was obtained from their water displacement volume in small calibrated vessels. Some length/weight regression equations obtained by this procedure are given by Pechen (1965). The different techniques cited give rise to considerable discrepancies among results obtained, as shown by Edmondson and Winberg (1971), who tabulated a number of regression equations obtained by various workers using different techniques.

Burns (1969) used a Cahn microbalance for obtaining accurate dry weight values in a number of *Daphnia* species. Regression equations for the length/weight relationship were derived from logarithmically transformed data for each species and for the pooled data. Similar studies on copepods were conducted by Burgis (1971, in press) and Herzig (1974). Some authors (Duncan, in press; Herzig, 1974) give only ranges of dry weight or use a small number of coarse size classes. Rotifers have remained almost unstudied by this method, a few direct weighings having been made by Doohan and Rainbow (1971) on *Keratella quadrata* and by Doohan (1973) on *Brachionus plicatilis*.

Dry weight determinations for selected entomostraca occur throughout the literature. Mostly, the main objective of these studies is to gain insight into metabolic activities such as filtering rate and respiration (Burns, 1969; Ganf and Blazka, 1974), phosphorus and ammonia uptake or release (Hargrave and Geen, 1968; Comita, 1968; Peters and Rigler, 1973; Jacobson and Comita, in press) or size-selective feeding (Bogdan and McNaught, in press). Dry weight values are further necessary for performing calorimetry. Specific dry weights for *Daphnia* and *Diaptomus* are to be found in Richman (1958, 1964) while Snow (1972) recently derived an equation directly relating dry weight to calorimetric values in *Daphnia rosea*. Reviewing biomass research in marine plankton is outside the scope of the present paper, but much useful information may be found in Lovegrove (1966), Conover (1968) and Conover and Corner (1968).

Material and Methods

All species weighed were sorted from samples collected in the field.

Balances. As a preliminary step, three types of balances were compared: a Sauter Type 414 analytical balance (sensitivity 10 μg), a Cahn Type 4100 Electrobalance (sensitivity 0.1 μg) and a Mettler ME 22/BA 25 Microbalance (sensitivity 0.1 μg).

Aliquots of the rotifer *Asplanchna priodonta*, all taken from the same sample, were used as test material. Using the same number of animals (usually 50), the microbalances were found to show good agreement (deviation ca. 5%), but greater deviations resulted from the use of the analytical balance (up to 50%), unless the number of animals was increased by a factor 50. For reasons of speed, automation and sensitivity (even in the higher weight ranges: automatic taring), the Mettler microbalance was routinely used in later work.

Working Procedure. After sorting the species from the samples, they were measured (total body length) under a dissecting microscope (larger instars) or a compound microscope (smaller instars, rotifers) and divided into size-classes. The mean length (for *Asplanchna* also volume) of each size-class was recorded, as well as the number measured. The size-classes were transferred to small glass vials, briefly washed with distilled water and pippeted into small aluminium boats that had been ovendried to constant weight (2 hrs at 110° C). Each boat was stored in a closed petri-dish, oven-dried for 2 hrs at 110° C, allowed to cool for 30 min in a dessicator and weighed on the scalepan of a Mettler microbalance.

The number of animals used per weighing varied according to the expected weight. Numbers were chosen so that each weighing would produce a minimum of 5 μg dry weight. For Cladocera, Copepoda, large rotifers, 1–50 animals proved sufficient, while 50–2000 animals were used in small rotifers.

Results and Discussion

Preservation of Animals

Only animals preserved in 4% formaldehyde were used. The period of preservation varied between a few minutes and several years, depending upon the sources from which animals were obtained.

Howmiller (1972) has recently questioned the value of weight estimates from small aquatic animals, using preserved specimens. He compared the action of 70% ethanol, 70% isopropanol and 4% formaldehyde on tubificids and chironomid larvae. As Howmiller's data would seem to have a bearing on the results of our work, we shall deal with them at some length. When re-ranking his data (dry weight as a percentage of fresh weight) on losses for Tubificidae, we obtain:

fresh	15.9%
4% formaldehyde	12.3%
water (freezing)	10.0%
ethanol	8.1%
isopropanol	6.3%

The loss is seen to be actually inhibited by formaldehyde, taking water as a standard, while in alcohols it is enormous. The phenomenon is easily understood by the nature of these preservatives: formaldehyde precipitates proteins and blocks eventual body pores; alcohols, conversely, are powerful solvents. One might therefore predict that, the smaller the animal and the thinner its body wall, the lower the losses in formaldehyde will be. Using alcohols, the reverse phenomenon may be expected. This is confirmed by Howmiller's data. Long-term losses in tubificids amount to 55% of fresh weight in ethanol, and only to 20% in formaldehyde. In sclerotized chironomids, a long-range loss of about 45% occurs with both preservatives.

Table 1

Asplanchna priodonta (1) June 1974		*Asplanchna priodonta* (2) September 1965	
Number weighed	Mean weight (μg)	Number weighed	Mean weight (μg)
25	0.48	50	0.50
50	0.52	100	0.48
50	0.50		
75	0.60		
100	0.52		
100	0.50		

Table 2. Regression equations for Cladocera ($W = a \cdot L^b$)

Species	Origin	This paper: Length mm[a], Dry weight µg	This paper: Length µm, Dry weight µg	Comparable literature data: Length mm, Dry weight mg (Burns, 1969)	Comparable literature data: Length mm, Fresh weight mg (Pechen, 1965)
Sididae					
Diaphanosoma brachyurum (Liévin)	(g)		$W = 1.76 \times 10^{-6}\ L^{2.11}$		
Daphniidae					
Daphnia ambigua Scourfield (1)	(a)		$W = 6.29 \times 10^{-7}\ L^{2.29}$		
Daphnia galeata Sars (2)	(a)		$W = 9.5 \times 10^{-8}\ L^{2.56}$		
Daphnia pulex Leydig (3)	(a)		$W = 2.4 \times 10^{-8}\ L^{2.77}$		
Daphnia magna Straus, Donk Lake (4)	(a)		$W = 1.89 \times 10^{-6}\ L^{2.25}$		
Daphnia magna Straus, River Sambre	(b)		$W = 4.88 \times 10^{-5}\ L^{1.80}$		
Daphnia (1)–(4) pooled			$W = 1.5 \times 10^{-8}\ L^{2.84}$		
Daphnia spec.					$W = 0.052\ L^{3.012}$
Daphnia pulex, ephippial	(a)		$W = 0.2 \times 10^{-9}\ L^{3.13}$	$W = 0.012\ L^{2.63}$	
Daphnia magna, ephippial	(a)		$W = 1.23 \times 10^{-7}\ L^{2.61}$	$W = 0.009\ L^{2.63}$	
Simocephalus vetulus (O.F.M.), Belgium 1967	(l)	$W = 4.0\ L^{3.81}$			
Simocephalus vetulus (O.F.M.), Belgium 1974	(k)	$W = 7.43\ L^{3.28}$			
Simocephalus vetulus (O.F.M.), Morocco 1971	(g)	$W = 3.36\ L^{3.44}$			
Ceriodaphnia quadrangula (O.F.M.)	(a)		$W = 1.70 \times 10^{-6}\ L^{2.26}$		
Ceriodaphnia reticulata (Jurine)	(g)		$W = 5.91 \times 10^{-6}\ L^{2.02}$		
Scapholeberis mucronata (O.F.M.)	(h)		$W = 8.9 \times 10^{-8}\ L^{2.70}$		
Moinidae					
Moina micrura Kurz	(i)	$W = 6.61\ L^{2.57}$			
Moina micrura, ephippial	(i)	$W = 9.81\ L^{3.39}$			
Moina mongolica Daday	(f)	$W = 4.67\ L^{2.13}$			
Moina mongolica (+2 eggs)	(f)	$W = 4.91\ L^{3.62}$			
Bosminidae					
Bosmina longirostris (O.F.M.)	(a)	$W = 26.6\ L^{3.13}$			
Bosmina longirostris (+4 eggs)	(a)	$W = 108.0\ L^{4.27}$			$W = 0.124\ L^{2.181}$

Table 2 (continued)

Chydoridae			
Chydorus sphaericus (O.F.M.)	(a)	$W = 89.43\ L^{3.93}$	
Chydorus sphaericus (+2 eggs)	(a)	$W = 124.23\ L^{4.08}$	
Alona rectangula Sars (+2 eggs)	(a)	$W = 29.65\ L^{3.48}$	
Alona affinis (Leydig) (+2 eggs)	(c)	$W = 15.92\ L^{3.84}$	
Alonella exigua (Lilljeborg)	(c)		$W = 1.70 \times 10^{-4}\ L^{1.39}$
Alonella exigua (+2 eggs)	(c)		$W = 1.35 \times 10^{-6}\ L^{2.26}$
Pleuroxus aduncus (Jurine)	(a)	$W = 35.6\ L^{4.03}$	
Acroperus harpae (Baird)	(j)		$W = 9.05 \times 10^{-3}\ L^{0.85}$
Acroperus harpae (+2 eggs)	(j)		$W = 1.30 \times 10^{-4}\ L^{1.56}$
Polyphemidae			
Polyphemus pediculus (L.) (+eggs)	(h)		$W = 2.46 \times 10^{-6}\ L^{2.15}$

(a)–(g): see Table 8; (h): Putse Moer, Belgium, June 1974; (i): Kanle Çesme, Turkey, July 1973; (j): Daiet Iffer, Morocco, July 1971; (k): Pond at Teralfene, Belgium, June 1974; (l): Lake Donk, Belgium, July 1967.

[a] Use of mm for length necessary when intercept involves negative integers above 10, not obtainable by current desk computers.

In our tests we mainly used the rotifer *Asplanchna priodonta*, a species closely allied to *Asplanchna brightwelli*, which was used in the regression analysis (see further). A comparison was made of dry weights obtained after briefly freezing, treatment with 70% ethanol and treatment with 4% formaldehyde. No differences were recorded between fresh-frozen animals and those preserved in formaldehyde for a variable number of days. Ethanol produced an exponential weight loss of 40% in 2 hrs, 56% in 4 hrs and 63% in 6 hrs. Long range weight losses in rotifers preserved in formaldehyde appear to be negligible as well, as indicated by the data in Table 1.

The first sample (1) was collected in a pond in Gent and weighed within 4 hrs after fixation in formaldehyde; the second sample (2) was collected in a lakelet near Gent and was preserved in formaldehyde for 9 years. All animals had a volume of about $1.1 \times 10^7\ \mu^3$. There was no significant weight difference between the two and, further, it is seen that as few as 25 animals suffice for obtaining an accurate mean individual weight. The reason for this stability in weight is, in our opinion, due to the almost instantaneous entrance of the fixative into the animal. Weight losses in small entomostraca are probably more closely related to the situation for the rotifers than for tubificids.

In *Daphnia pulex*, we found a 50% weight loss in 24 hrs when killing the animals in 70% ethanol but virtually no loss in 4% formaldehyde. Although it is likely that some long-range losses occur, they might not exceed 5–10%.

Cladocera

Twenty-eight species, representing 19 genera, have been studied. The majority could be divided into size-classes and a regression equation computed from the

Table 3. Dry weight data for embryo's and eggs in Cladocera and for adults in rare species or species that could not be dealt with in size-classes

	Origin	Embryo		Egg	
		Mean length (mm)	Mean weight (μg)	Mean length (mm)	Mean weight (μg)
Diaphanosoma brachyurum (Liévin)	(g)	0.279	0.67	—	—
Daphnia ambigua Scourfield	(a)	0.252	0.67	0.180	0.62
Daphnia galeata Sars	(a)	0.288	0.56	0.198	0.71
Daphnia pulex Leydig	(a)	0.452	2.75	0.297	2.40
Daphnia magna Straus	(a)	0.603	7.62	0.372	8.00
Scapholeberis mucronata (O.F.M.)	(h)	0.247	0.72	0.186	0.78
Simocephalus vetulus O.F.M.)	(k)	0.379	1.92	0.189	1.60
Ceriodaphnia reticulata (Jurine)	(g)	0.284	0.31	0.180	0.26
Ceriodaphnia quadrangula (O.F.M.)	(a)	0.194	0.39	0.162	0.35
Moina micrura Kurz	(i)	0.358	0.65	—	—
Moina mongolica Daday	(f)	0.504	2.60	—	—
Moina macrocopa (Straus)	(c)	0.378	0.77	—	—
Bosmina longirostris (O.F.M.)	(a)	0.234	0.32	0.162	0.20

	Origin	Egg-bearing females		Females without eggs	
		Mean length (mm)	Mean weight (μg)	Mean length (mm)	Mean weight (μg)
Eurycercus lamellatus (O.F.M.)	(c)	—	—	2.376 0.746	157.0 3.87
Alona costata (Sars)	(c)	0.441	1.5	0.441	1.0
Leydigia quadrangularis (Leydig)	(a)	0.630	3.0	0.702	2.0
Graptoleberis testudinaria (Fischer)	(j)	0.459	2.6	0.404	1.4
Alonella nana (Baird)	(c)	0.234	0.42	0.198	0.31
Dunhevedia crassa King	(j)	0.450	1.2	0.450	1.0
Acantholeberis curvirostris O.F.M.	(h)	1.188	13.2	1.008	7.6
Sida crystallina (O.F.M.)	(j)	2.430	112.0	—	—
Moina macrocopa (Straus)	(c)	—	—	1.020	7.1

The letters refering to the origin of the samples are the same as in Table 8.

logarithmically transformed data. In forms where females carry a variable number of eggs, the broodpouch was emptied before weighing. One species in which this could not be done without damaging the specimens was *Polyphemus pediculus*. In 6 species, ephippial females were available, 4 among which could be treated in weight classes (Figs. 2 and 3).

Eggs and embryos in various stages were obtained in 14 species and were measured and weighed apart. They are not included in the regressions, but the values are given in Table 3.

A set of length/weight values drawn from the equations is given in Table 4, where the representative lengths span the size range for each species but are not measured values.

Table 4. Representative length/weight data (mm, μg) for various Cladocera (females without eggs, unless stated otherwise in footnotes)

Length	*Daphnia ambigua* Scourfield	*Daphnia galeata* Sars	*Daphnia pulex* Leydig	*Daphnia magna* Straus	
				Donk Lake	Sambre River
0.500	0.97	0.75	—	—	—
0.750	2.46	2.12	2.25	—	—
1.000	4.77	4.43	5.01	—	—
1.250	7.95	7.85	9.30	—	—
1.500	—	12.49	15.41	26.07	25.14
1.750	—	18.53	23.63	36.89	33.18
2.000	—	26.06	34.23	49.79	42.19
2.250	—	—	47.41	64.83	52.11
2.500	—	—	63.59	82.26	63.57
2.750	—	—	82.63	101.71	74.72
3.000	—	—	—	123.82	87.45
3.250	—	—	—	148.42	101.09
3.500	—	—	—	175.15	115.41
3.750	—	—	—	204.58	130.68
4.000	—	—	—	236.49	146.75

	Moina micrura Kurz		*Moina mongolica* Daday		*Simocephalus vetulus* (O.F.M.), 1967	*Simocephalus vetulus* (O.F.M.) 1971	*Simocephalus vetulus* (O.F.M.), 1974
	(1)	(3)					
0.600	1.18	—	1.58	—	0.57	0.58	1.39
0.800	3.73	—	2.91	—	1.71	1.55	3.57
1.000	6.61	9.81	4.67	—	4.00	3.36	7.43
1.200	10.55	18.19	6.87	9.49	8.00	6.29	13.50
1.400	—	—	9.54	16.58	14.41	10.70	22.39
1.600	—	—	—	—	23.99	16.95	34.71
1.800	—	—	—	—	37.54	25.41	51.02
2.200	—	—	—	—	80.58	50.68	98.46
2.400	—	—	—	—	112.50	68.53	131.21
2.600	—	—	—	—	152.98	90.47	170.93

	Ceriodaphnia reticulata (Jurine)	*Ceriodaphnia quadrangula* (O.F.M.)	*Diaphanosoma brachyurum* (Liévin)	*Scapholeberis mucronata* (O.F.M.)	*Polyphemus pediculus* (L.)
0.400	1.04	1.32	0.53	0.93	—
0.500	1.64	2.19	0.85	1.71	1.55
0.600	2.37	3.30	1.25	2.79	2.29
0.700	3.23	4.68	1.74	4.23	3.20
0.800	4.23	6.34	2.30	6.07	4.26 (2)
0.900	5.36	8.27	2.95	8.33	5.48 (2)
1.000	6.64	10.51	3.68	11.08	6.88 (2)
1.100	8.03	13.01	4.49	14.30	—
1.200	9.58	15.86	5.40	18.11	—

Table 4 (continued)

	Chydorus sphaericus (O.F M.)		*Bosmina longirostris* (O F M.)		*Pleuroxus aduncus* (Jurine)	*Alonella exigua* (Lilljeborg)		*Alona rectangula* Sars	*Alona affinis* (Leydig)	*Acroperus harpae* (Baird)	
	(1)	(2)	(1)	(2)		(1)	(2)			(1)	(2)
0.200	—	—	0.17	—	—	0.26	—	—	—	—	
0.250	0.39	—	0.35	—	—	0.36	—	—	—	—	
0.300	0.79	—	0.62	—	—	0.46	0.52	0.45	—	—	
0·350	1.45	1.71	1.00	1.21	—	0.57	0.80	0.77 (2)	—	—	
0·400	2.44	2.94	1.52	2.05	0.88	0.69	1.15	1.22 (2)	0.47	1.52	
0·450	3.87	4.75	2.19	3.25	1.42	—	—	—	0.74	1.68	
0·500	5.87	7.33	3.05	4.93	2.18	—	—	—	1.11	1.84	
0·550	8.00	10.77	4.09	7.14	3.18	—	—	—	1.60	1.99	2.47
0·600	—	—	—	—	4.53	—	—	—	2.24	2.15	2.83
0.650	—	—	—	—	6.27	—	—	—	3.05	2.30	3.21
0·700	—	—	—	—	—	—	—	—	4.04 (2)	2.45	3.60
0.750	—	—	—	—	—	—	—	—	5.27 (2)	2.60	4.01

(1) Females without eggs; (2) females with eggs; (3) ephippial females.

Table 5. Representative length/weight data for two ephippial *Daphnia*-species, compared to Burns' (1969) data for egg-bearing females and to Pechen's (1965) data on fresh weight in *Daphnia* sp.

Length (mm)	*Daphnia pulex* Leydig (weight: mg)			*Daphnia magna* Straus		
	Lake Donk	Burns (1969)	Pechen (1965)	Lake Donk	Burns (1969)	Pechen (1965)
0.750	0.002	0.006	0.022	—	—	—
1.000	0.004	0.012	0.052	—	—	—
1.250	0.010	0.022	0.102	—	—	—
1.500	0.018	0.035	0.176	0.024	0.026	0.176
1.750	0.029	0.052	0.280	0.035	0.039	0.280
2.000	0.044	0.074	0.419	0.050	0.055	0.419
2.250	0.063	0.101	0.597	0.068	0.075	0.597
2.500	0.088	0.134	0.822	0.089	0.100	0.822
2.750	—	—	—	0.114	0.128	1.032
3.000	—	—	—	0.144	0.161	1.421
3.250	—	—	—	0.177	0.199	1.812

The genus *Daphnia* is represented by four species. A mean equation (Fig. 1) drawn from all data and based on females without eggs gives less scatter than Burns' (1969) analogous equation for females with eggs. However, because of considerable differences between species' equations (Table 2), it is clearly up to the user of such equations to choose between a genus-level or a species-level approach. In either approach, an egg or embryo count is necessary in order to find the weight that should be added to the body weight determined from the equations.

In *Daphnia pulex* and *Daphnia magna*, where ephippial females were available (Fig. 2), we made a comparison with Burns' data for eggbearing females and with Pechen's (1965) data for fresh weight in *Daphnia* sp. (Table 5). There was close

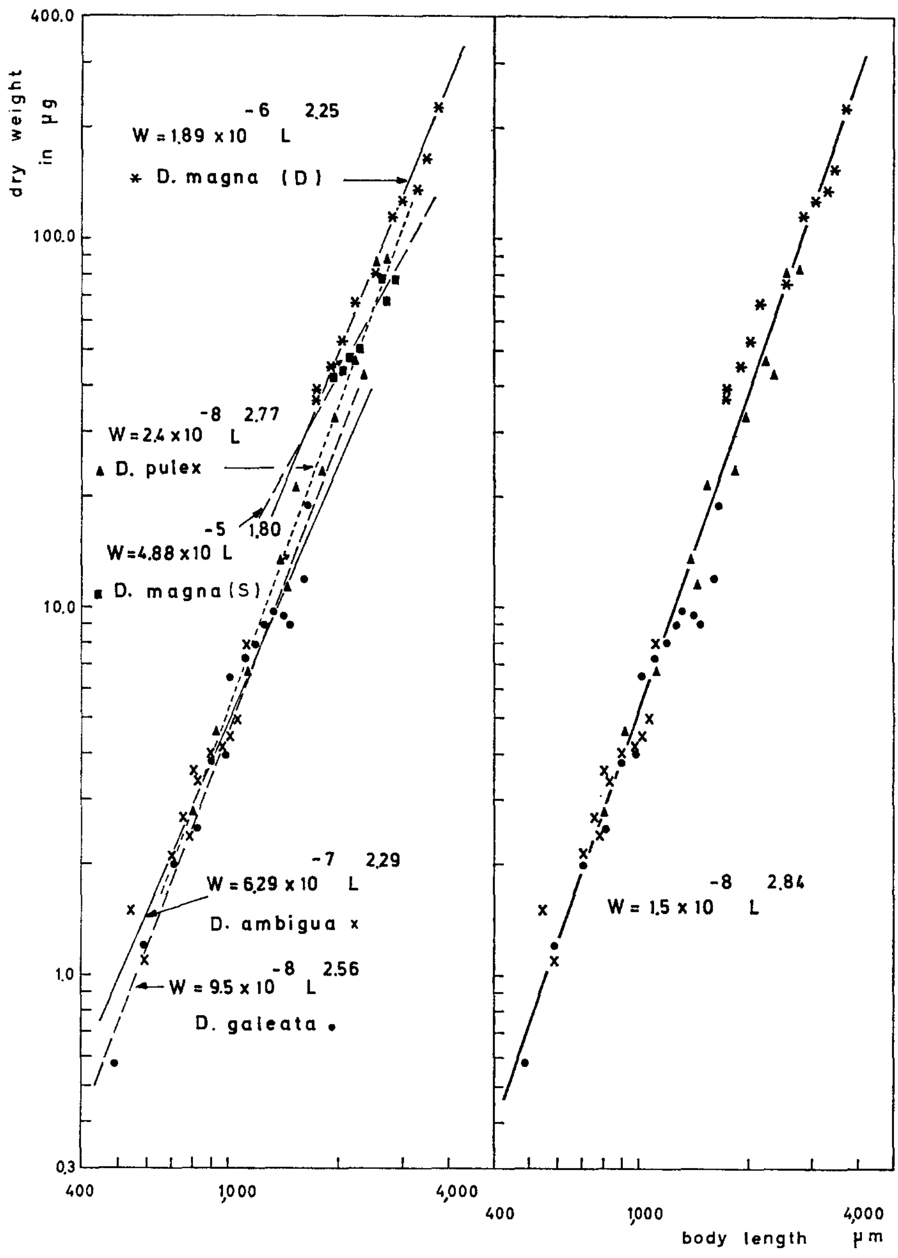

Fig. 1. Relation between body length and body weight in 4 *Daphnia*-species. Left: individual species regression lines. For *Daphnia magna*, 2 different populations are included; (*D*) Donk Lake, (*S*) Sambre River. Right: pooled data and pooled regression line; all animals without eggs

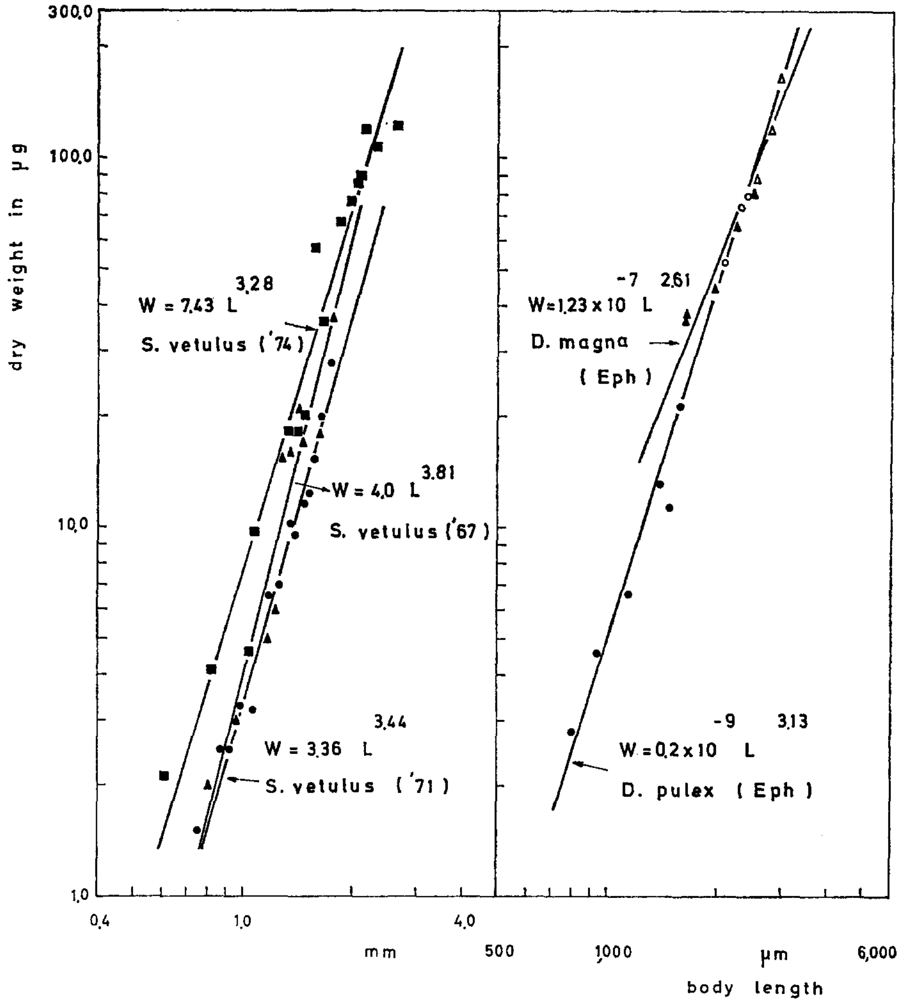

Fig. 2. Relation between body length and body weight. Left: *Simocephalus vetulus*, 3 populations of different preservation time (1967, 1971, 1974) and of different origin (see text and Table 2); all animals without eggs. Right: 2 species of *Daphnia*. Open circles and triangles: ephippial females; full circles and triangles: specimens without ephippia

agreement with Burns' data for *Daphnia magna*, but not for *D. pulex*. Pechen's values are close to 10 times ours for *D. pulex*; a similar but less consistent relationship exists with our *D. magna* from Lake Donk (Flanders, Belgium). This supports the often used fresh weight/dry weight ratio of 10:1.

That such regression formulae should not be universally applied without reservation is proven by a comparison of *D. magna* from Lake Donk with *D. magna* from the river Sambre, Belgium (Table 2). The latter is a heavily polluted river carrying considerable organic load and a wide variety of heavy metals. The dry weights obtained from the two equations diverge with increasing length and differ considerably in the longest animals. The lower weight of *D. magna* in the polluted river is likely attributable, although probably only in part, to the inhibition of biomass accumulation by the toxicants. It therefore seemed advisable not to include this population in the general regression equation, although Fig. 1 shows that, in doing so, the equation would not have been significantly affected. Another factor that perhaps contributes is that the sector of Lake Donk where *Daphnia magna* occurs (near the outlet) is swampy and has some aquatic vegetation, while the concrete walls of the river Sambre are devoid of macrophytes.

An analogous phenomenon appears in three series of *Simocephalus vetulus* treated (Fig. 2). This morphologically variable animal commonly occurs in ponds and the littoral of lakes, and variability is probably biotope-dependent. If the two Belgian populations are compared (Lake Donk, June 1967, animals preserved for 7 years in formaldehyde; Pond at Teralfene, Flanders, June 1974, animals treated freshly), weight differences are greatest in the smaller instars, but decline with increasing length to less than 10% in the largest animals. Weight losses following fixation are an unlikely explanation for this phenomenon. Rather it would appear that trophic differences in the biotope cause the respective populations to grow at a different rate.

Much greater differences were found when these two populations were compared to one sampled in July 1971 in Aguelman-de-Sidi-Ali (a lake at 2000 m altitude in the Atlas mountains, Morocco, characterized by steep, rocky shores without littoral vegetation) where the weigths were almost half those of the 1974 Belgian population.

Fig. 2 illustrates that the differences in weight between populations of a species may be described by slope as well as by intercept, depending upon the origin of the sample. Seasonal (Green, 1956), altitudinal and geographical factors are frequently held responsible for this. Differences in the physical conditions of the habitat, such as those that may force a normally littoral species to behave more like a limnetic one, might however be far more important. A littoral, phytophilous species that switches to a limnetic way of life, spends more energy in swimming, and consumes part of its biomass should therefore weigh less for the same length.

In another case, two daphniids, *Ceriodaphnia reticulata* and *Ceriodaphnia quadrangula*, of similar habitus, differ more than would be expected on the basis of the *Daphnia* data (Fig. 3). *C. reticulata,* which is the larger species of the two, weighs relatively less than *C. quadrangula*. One sample came from Lake Donk, Belgium, the other from Aguelman-de-Sidi-Ali, Morocco. Both species are normally littoral ones.

One of the strictly pelagic cladocerans collected in Aguelman-de-Sidi-Ali is *Diaphanosoma brachyurum*. If compared to other species in the same length range, such as *Ceriodaphnia* and *Scapholeberis* (Table 4), it proves to be an extremely light animal. Our range of weights agrees closely to that given by Herzig (1974) for an Austrian population from the lowland Neusiedler See. In limnetic species, altitudinal differences seem to have little effect on the length/weight relationship.

This is further illustrated by two species of *Moina* (Fig. 3). *Moina mongolica* is limnetic in saline lakes (Aci Göl, Turkey, June 1973), while *Moina micrura* is a pond species of worldwide occurrence. Again, the regressions for both species differ considerably, and the larger *M. mongolica* is lighter than the smaller *M.*

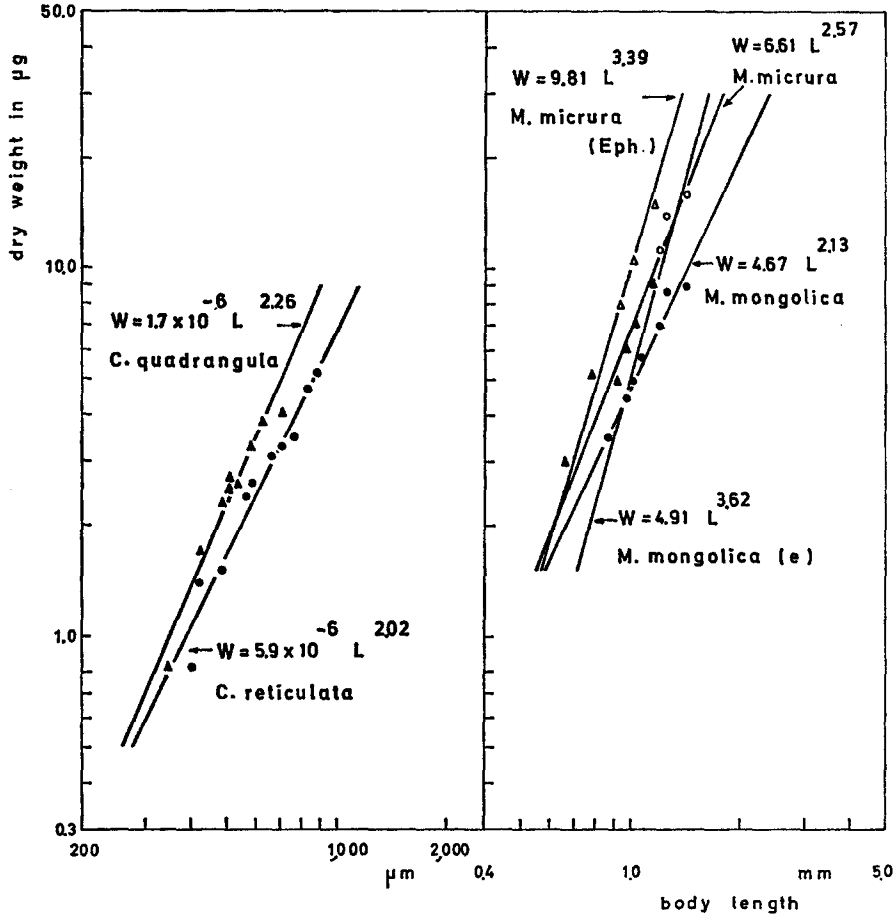

Fig. 3. Relation between body length and body weight. Left: 2 species of *Ceriodaphnia*, all without eggs. Right: 2 species of *Moina*, with and without ephippia (*Eph*) or eggs (*e*). Full circles and triangles: specimens without eggs; open circles and triangles: ephippial or egg-bearing females

micrura. A few data for another pond species, *M. macrocopa*, fall within the range of *M. micrura*.

Scapholeberis mucronata (O.F.M.) (Belgium, June 1974), conversely (Fig. 4), is heavier than all other daphniids in the length range of 0.4–1.2 mm (Table 4). It is a highly specialized, hyponeustic species occuring in ponds and in the weedy littoral of lakes.

As far as the non-chydorid cladocera are concerned, results generally indicate that littoral species are relatively much heavier than limnetic species and that, even within a species, a relative shift between these two ways of living is reflected in their biomass. *Polyphemus pediculus*, a species living in oligotrophic lakes but found in Belgium in dystrophic ponds (North-East Belgium, June 1974) takes an intermediate position (Fig. 4, Table 4).

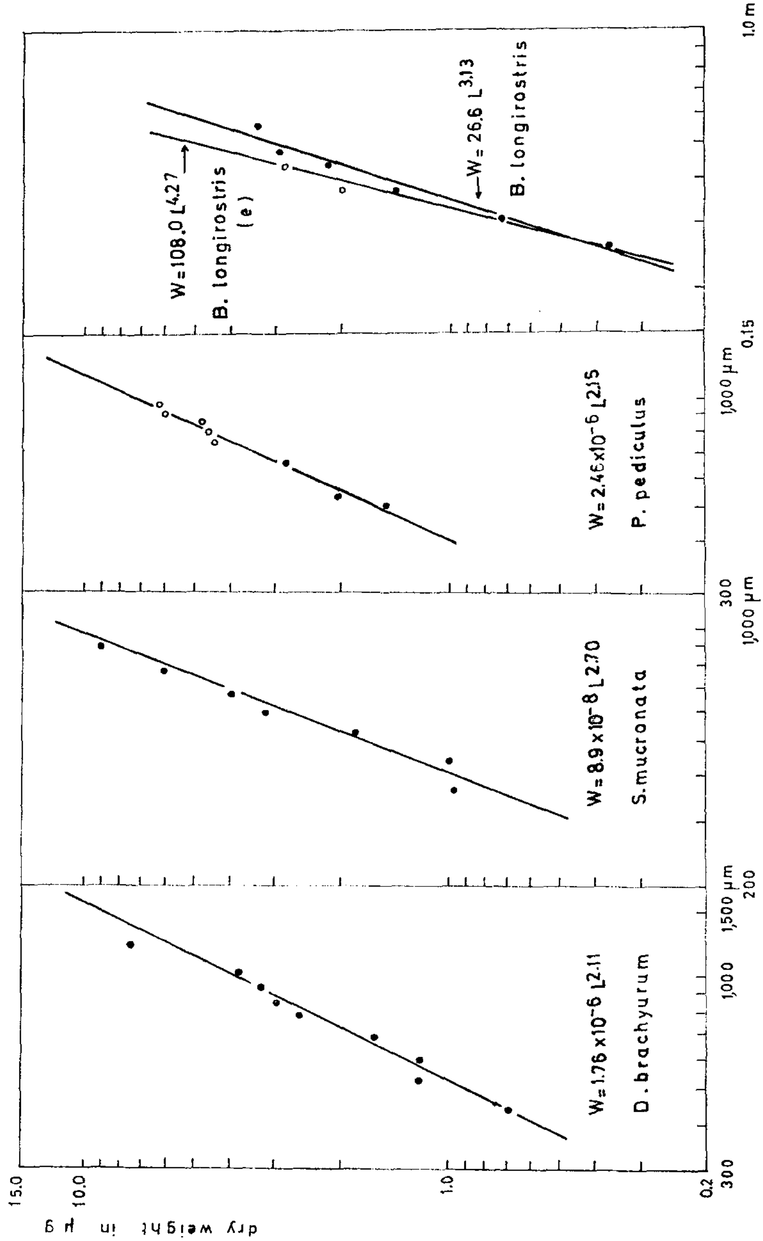

Fig. 4. Relation between body length and body weight. Left: *Diaphanosoma brachyurum* and *Scapholeberis mucronata*; all animals without eggs. Right: *Polyphemus pediculus* and *Bosmina longirostris*: with and without eggs. Full circles: specimens without eggs; open circles: eggbearing females

An interesting case is provided by *Bosmina longirostris* (O.F.M.), a species of large eutrophic ponds, which is replaced by *Bosmina coregoni* in the pelagial of large lakes. The length/weight relationship in *B. longirostris* (Fig. 4, Table 4) is indeed that of a littoral rather than of a limnetic species, and it would be interesting to compare it to the morphologically related *B. coregoni*. Pechen's (1965)

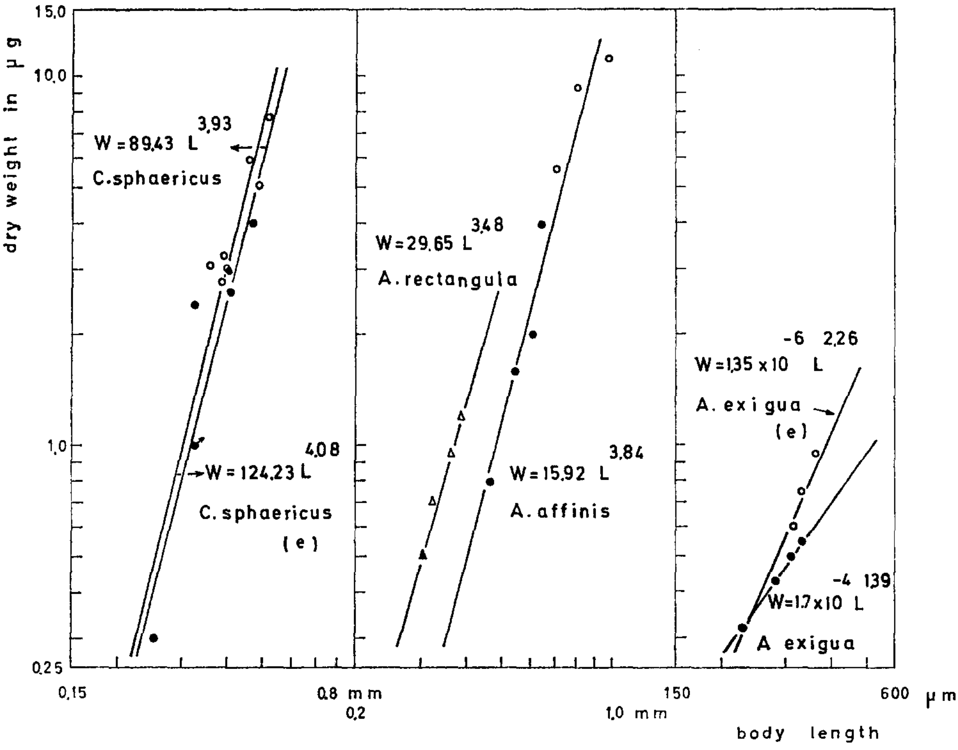

Fig. 5. Relation between body length and body weight. Left: *Chydorus spaericus*; regression lines for animals without eggs and for animals with eggs (*e*). Middle: 2 *Alona*-species. Right: *Alonella exigua*; regression lines for animals with (*e*) and without eggs. Open circles and triangles: eggbearing females; full circles and triangles: animals without eggs

equation for *B. longirostris* does not compare well with ours, except in large animals (Table 2).

As all chydorids are littoral, periphytic or pond species, one would expect them to have relatively high weights. This is confirmed by *Chydorus sphaericus* (O.F.M.), by 2 *Alona*-species and by *Pleuroxus aduncus* (Fig. 5, Table 4). However, two chydorids, *Alonella exigua* and *Acroperus harpae*, weigh relatively less and tend to fall within the range of limnetic species. They are, however, much smaller than the other chydorids studied. The 2 *Alona*-species have a regression equation (Fig. 5, Table 2) that is quite different, as in *Ceriodaphnia*.

Among chydorids, and because the females carry only two big eggs, it made sense to compare parallel series of females with and without eggs. The slope of the regression equation is greatly influenced by this, even more than in the case of *Daphnia* and *Moina* (Fig. 5). In non-gravid females, exponents in the range of 3.0 occur. These increase to over 4.0 if egg-bearing females are considered. The weight of individual eggs, compared to the weight of females, is indeed very high (Table 3). Table 3 also gives weight data for species that were available as adults only or in which not enough size-classes were available to perform a regression analysis.

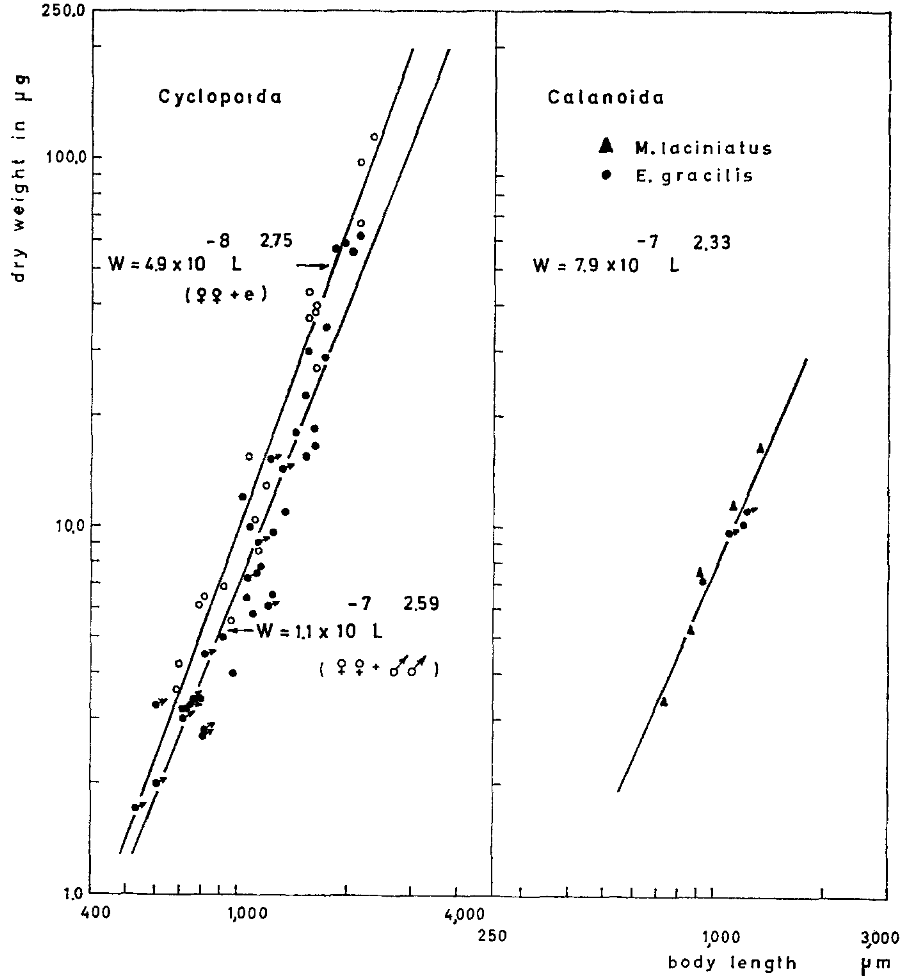

Fig. 6. Relation between body length and body weight. Left: adult Cyclopoida; a separate regression was computed for ovigerous females of various genera and species (♀♀+*e*) and for females without eggs and males (♀♀+♂♂). Right: Calanoida, pooled equation for adult *Mixodiaptomus laciniatus* and *Eudiaptomus gracilis*, including males but without ovigerous females

In conclusion, it appears that one can infer more about the relative weight of cladocerans by their ecology than by their taxonomic relationship, although there are exceptions among the Chydoridae, in which the body proportion may in part contribute to the phenomenon (however, see: Rotatoria).

Copepoda

The uniformity in shape within the three suborders of this group makes it tempting to derive one length/weight regression equation per suborder. Weights were determined for a number of Cyclopoida, including most of the genera of

Table 6. Regression equations for Copepoda

Adult Cyclopoida, including females with eggs (μm, μg):	$W = 4.9 \times 10^{-8} L^{2.75}$
Adult Cyclopoida, females with eggs excluded (μm, μg):	$W = 1.1 \times 10^{-7} L^{2.59}$
Burgis (in press), pooled equation (μm, μg):	$W = 2.2 \times 10^{-8} L^{2.82}$
Klekowski and Shushkina (1966), fresh weight (mg, mm):	$W = 0.055 L^{2.73}$
Copepodites plus nauplii (μm, μg):	$W = 1.10 \times 10^{-5} L^{1.89}$
Burgis (in press), copepodites plus nauplii (μm, μg):	$W = 1.17 \times 10^{-6} L^{2.20}$
Calanoida, pooled equation (μm, μg):	$W = 7.9 \times 10^{-7} L^{2.33}$
(mm, mg):	$W = 0.0077 L^{2.33}$
Herzig (1974), Arctodiaptomus males (mm, mg):	$W = 0.0098 L^{2.3}$
Herzig (1974), Arctodiaptomus females (mm, mg):	$W = 0.0096 L^{3.47}$
Harpacticoida, pooled equation (mm, μg):	$W = 12.51 L^{4.40}$

Comparison of representative length/weight data (mm, μg) with literature sources cited above

Length	Copepodites		Adult Cyclopoida			
	This paper	Burgis (in press)	Females with eggs (this paper)	Females without eggs (this paper)	Burgis (in press)	Klekowski and Shushkina (1966) fresh weight
0.500	1.41	1.01	—	—	—	—
0.600	1.99	1.51	—	—	—	—
0.700	2.66	2.12	—	—	—	—
0.800	3.42	2.85	4.95	3.74	3.38	29.9
0.900	4.27	3.69	6.84	5.07	4.71	41.4
1.000	5.22	4.65	9.16	6.68	6.35	55.0
1.100	6.24	5.73	11.88	8.53	8.28	71.1
1.200	—	—	15.13	10.70	10.60	90.3
1.400	—	—	23.14	15.97	16.38	137.6
1.600	—	—	33.45	22.59	23.87	198.1
1.800	—	—	46.23	30.63	33.24	273.0
2.000	—	—	61.91	40.32	44.80	364.5
2.200	—	—	80.32	51.52	58.46	471.7
2.400	—	—	102.23	64.65	74.82	599.0

Length	Calanoida			Harpacticoida
	This paper	Herzig (1974) males	Herzig (1974) females	This paper
0.500	—	—	—	0.59
0.600	2.33	3.02	1.63	1.32
0.700	3.34	4.31	2.78	2.50
0.800	4.56	5.86	4.42	4.68
0.900	6.00	7.68	6.65	7.85
1.000	7.68	9.80	9.60	12.51
1.100	9.57	12.18	13.32	—
1.200	11.73	14.89	18.05	—
1.300	14.15	17.92	23.87	—
1.400	16.80	21.23	30.82	—

Table 7. Summary of dry weight data on the Copepoda

	Origin	Females with eggs		Females without eggs		Males		Copepodites		Egg-sack	Eggs
		mean length (mm)	Mean weight (µg)	(mm)	(µg)	(mm)	(µg)	(mm)	(µg)	(µg)	(µg)
Calanoida											
Eudiaptomus gracilis (Sars)	(b)	1.320	14.9	1.221	10.2	1.122	9.9	—	—	3.1	—
Mixodiaptomus laciniatus (Lilljeborg)	(g)	—	—	0.947	7.7	—	—	—	—	—	—
Cyclopoida											
Acanthocyclops robustus (Sars)	(b)	1.125	10.4	1.143	7.5	0.819	2.8	—	—	—	—
Cyclops abyssorum (Sars)	(g)	1.674	20.7	1.348	10.3	1.224	6.1	0.733	2.2	—	—
Cyclops strenuus (Fischer)	(e)	1.602	38.3	1.596	26.7	1.080	7.3	1.148 0.670	16.1 2.0	5.65	—
Diacyclops bicuspidatus (Claus)	(e)	1.206	13.0	1.098	10.0	0.756	3.3	—	—	—	—
Eucyclops serrulatus (Fischer)	(e)	1.098	15.4	1.026	12.0	0.774	3.4	—	—	2.0	—
Macrocyclops albidus (Jurine)	(a)	1.584	43.0	1.632 1.413	31.8 16.6	1.229	11.3	—	—	6.4	—
Macrocyclops fuscus (Jurine)	(a)	2.196	67.2	1.922	45.4	1.224	15.3	—	—	—	0.24
Megacyclops viridis (Jurine)	(a)	2.276	114.3	2.088	61.0	—	—	—	—	19.2	—
Mesocyclops leuckarti (Claus)	(a)	1.170	8.8	1.128	7.2	0.810	2.7	0.900	3.7	0.55	—
Metacyclops problematicus Dumont	(c)	0.993	5.5	0.993	4.0	0.726	3.0	—	—	0.75	—
Paracyclops fimbriatus (Fischer)	(c)	0.698	4.2	0.678	3.6	0.604	3.3	—	—	—	—
Thermocyclops hyalinus (Rehberg)	(a)	0.924	6.9	0.924	5.0	0.825	4.5	0.759	3.0	0.95	0.12
Tropocyclops prasinus (Fischer)	(b)	0.797	6.3	0.769	3.3	0.549	1.8	—	—	1.35	—
Harpacticoida											
Canthocamptus staphylinus (Jurine)	(e)	—	—	0.918 0.668	8.0 2.8	0.864	7.3	0.468	2.3	—	—
Cletocamptus retrogressus (Schmankewitch)	(f)	0.720	2.8	0.652	1.4	0.558	1.5	0.369	1.2	0.25	—

The letters refering to the origin of the samples are the same as in Table 8.

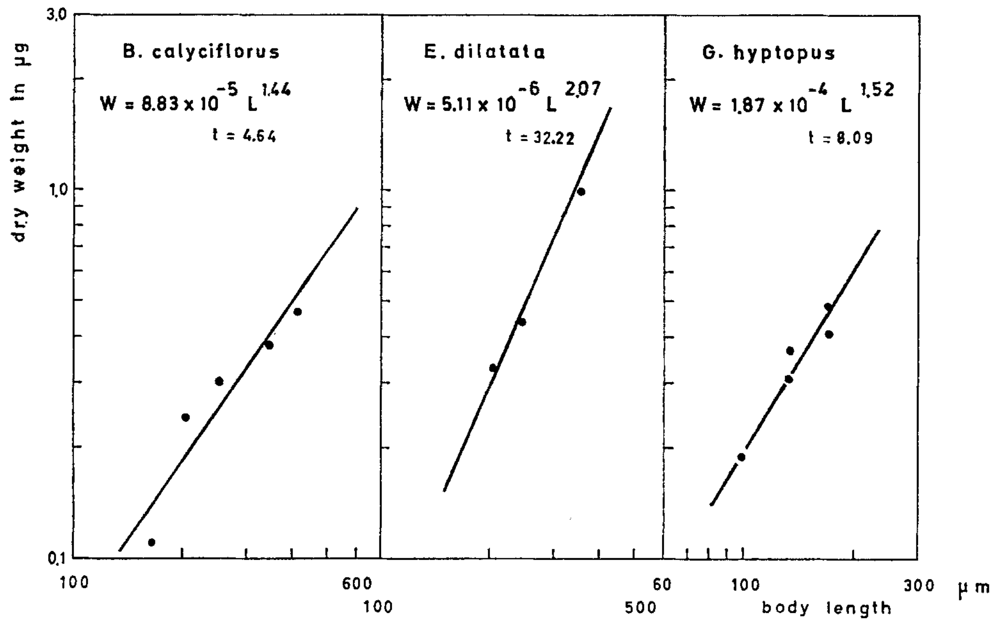

Fig. 7. Relation between body length and body weight in Rotifera. Left: *Brachionus calyciflorus*. Middle: *Euchlanis dilatata*. Right: *Gastropus hyptopus*. $t = \frac{b}{s_b}$ (b: slope, s_b: sample standard deviation of the regression coefficient). All regression coefficients are significantly different from zero ($P < 0.01$)

common occurrence throughout the world. With few exceptions, adult males and adult females with and without eggs were treated. Ontogenetic series were available in two representatives of the large-sized genus *Cyclops* s. str. As the size of the copepodites in these overlaps with the adults in most other genera, we pooled all data and computed a general regression equation. This proved unsatisfactory, partly because of the weight of the egg-sacs in ovigerous females. Therefore, two equations were derived, one with and one without ovigerous females (Fig. 6).

The equations differ by slope and intercept, and the males fall into the range of the second equation. The approach is still rather rough, by no way as refined as in the Cladocera, but wherever a quick assessment of the standing crop of a diverse cyclopoid fauna is necessary, it may serve well.

Burgis (in press) computed a similar equation for pooled stages of *Cyclops vicinus*, *C. vernalis* and *C. viridis*. A comparison with her equation including females with and without eggs is given in Table 6. Good agreement is found with our equation for females without eggs. A further refinement is obtained by regressing only the copepodites of *Cyclops abyssorum* and *C. strenuus*. It closely agrees with Burgis' similar equation for the related *C. vicinus* (Table 6).

An equation for computing fresh weight in Cyclopoida from length data is given by Klekowski and Shushkina (1966). Results herefrom are compared with our equation (Table 6), and show a fresh weight/dry weight relationship of 11%–12%, well comparable to the same relationship in *Daphnia*.

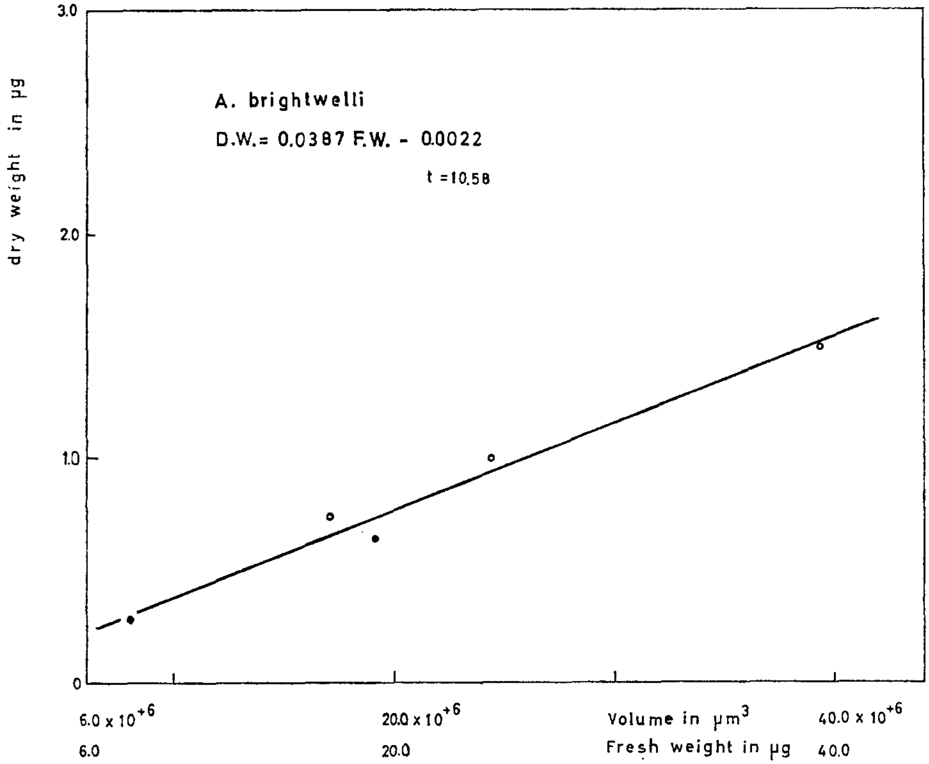

Fig. 8. Relation between body volume (fresh weight, *FW*) and dry weight (*DW*) in *Asplanchna brightwelli*. Full circles: females without embryos; open circles: females containing one or more embryos (b, s_b, t: see Fig. 8). The regression coefficient is significantly different from zero ($P < 0.01$)

In calanoids, we pooled *Mixodiaptomus laciniatus* and *Eudiaptomus gracilis* (Fig. 6), and the regression equation seems satisfactory. It was compared to Herzig's (1974) equation for *Arctodiaptomus spinosus* (Table 6) and a tolerably good agreement was found with *A. spinosus* males but not with the females. Future research on more Calanoida thus appears necessary.

Similarly, the two species of harpacticoids available (*Canthocamptus staphylinus* and *Cletocamptus retrogressus*) were pooled, but the common regression equation obtained (Table 6) should certainly be compared with results obtained from other species.

Table 7, finally, gives a summary of data on Copepoda and shows that, for a comparable length, littoral Copepoda tend to be heavier than limnetic ones, as in the Cladocera.

Rotatoria

In 4 of the larger species a length/weight regression equation of the exponential type was calculated (Fig. 7). If compared to similar equations for the Cladocera and Copepoda, they are remarkable for their much smaller slope.

In the case of *Asplanchna brightwelli*, the ellipsoidal shape of contracted animals made an accurate volume determination possible, and a linear regression of dry weight/volume was carried out (Fig. 8). Assuming a density not significantly different from 1.0, the equation reflects the dry weight/wet weight ratio which is, in this case, 3.9%.

On the whole, 27 species were studied. Most of the genera represented are important and sometimes dominant in natural waters of the world. Again, limnetic species tend to be lighter than non-limnetic ones. This is particularly obvious

Table 8. Summary of dry weight data on the Rotatoria

	Origin of animals		Dry weight (μg) and numbers weighed (n)	Egg weight (μg)
Asplanchna brightwelli Gosse	Rissani, Morocco, July 1971		0.28–1.5, see regression equation	
Brachionus angularis Gosse	University Pond, Gent, June 1974	(b)	0.40 ($n = 50$) 0.46 ($n = 100$) 0.54 ($n = 100$)	0.07
Brachionus calyciflorus (Pallas)	Sambre River, Belgium, 1973	(c)	0.11–0.47, see regression equation	0.12
Brachionus urceolaris O.F.M.	Sambre River, Belgium, 197^{7}3	(c)	0.20 ($n = 150$) 0.20 ($n = 40$) 0.12 ($n = 200$)	0.08
Brachionus quadridentatus Hermann	Sambre River, Belgium, 1973	(c)	0.42 ($n = 50$) 0.32 ($n = 50$)	0.10
Dicranophorus caudatus (Ehrbg)	Sambre River, Belgium, 1973	(c)	0.45 ($n = 100$)	
Euchlanis dilatata Ehrbg	Lake Donk, Belgium, Sept. 1971		0.30–1.0, see regression equation	
Filinia longiseta Ehrbg	Pond at Patan, Nepal, May 1973	(d)	0.48 ($n = 200$) 0.42 ($n = 100$)	
Floscularia ringens (Linné)	Sambre River, Belgium, 1973	(c)	1.1 ($n = 97$)	
Gastropus hyptopus (Ehrbg)	Wellemeersen, Belgium, May 1974	(e)	0.19–0.50, see regression equation	
Hexarthra fennica (Levander)	Aci Göl, Turkey, July 1973	(f)	0.64 ($n = 100$) 0.56 ($n = 200$)	
Hexarthra mira (Hudson)	Ag. Sidi Ali, Morocco, July 1971	(g)	0.85 ($n = 100$) 1.04 ($n = 100$)	
Keratella cochlearis (Gosse)	University Pond, Gent, June 1974	(b)	0.11 ($n = 350$)	
Keratella quadrata (O.F.M.)	University Pond, Gent, June 1974	(b)	0.32 ($n = 250$) 0.35 ($n = 100$)	
Lepadella ovalis (O.F.M.) (mean length: 135 μm)	Wellemeersen, Belgium, May 1974	(e)	0.31 ($n = 100$)	
Lepadella patella (O.F.M.) (mean length: 90 μm)	Wellemeersen, Belgium, May 1974	(e)	0.15 ($n = 180$)	
Mytilina mucronata (O.F.M.)	Wellemeersen, Belgium, May 1974	(e)	0.50 ($n = 100$)	
Polyarthra sp. div.	Lake Donk, Belgium, July 1971	(a)	0.74 ($n = 200$)	
Rotaria neptunia (Ehrbg)	Sambre River, Belgium, 1973	(c)	0.76 ($n = 100$) 0.72 ($n = 50$)	
Rotaria rotatoria (Pallas) + *Philodina roseola* Ehrbg	Sambre River, Belgium, 1973	(c)	0.22 ($n = 200$) 0.20 ($n = 50$) 0.25 ($n = 2000$)	

Table 8 (continued)

	Origin of animals		Dry weight (μg) and numbers weighed (n)	Egg weight (μg)
Stephanoceros fimbriatus (Goldfuß)	Sambre River, Belgium, 1973	(c)	1.1 ($n=55$)	
Synchaeta sp.	University Pond, Gent, June 1974	(b)	0.27 ($n=200$) 0.26 ($n=100$)	
Testudinella patina (Hermann)	Wellemeersen, Belgium, May 1974	(e)	1.2 ($n=180$) 1.2 ($n=200$) 1.1 ($n=800$)	
Trichocerca longiseta (Schrank) (mean length: 580 μm)	Wellemeersen, Belgium, May 1974	(e)	0.70 ($n=50$)	
Trichocerca longiseta (Schrank) (mean length: 370 μm)	Wellemeersen, Belgium, May 1974	(e)	0.40 ($n=50$) 0.36 ($n=50$) 0.35 ($n=50$) 0.34 ($n=50$)	
Trichocerca rattus (O.F.M.) (mean length: 123 μm)	Wellemeersen, Belgium, May 1974	(e)	0.10 ($n=70$)	

in the genus *Brachionus*, where *B. urceolaris* (limnetic) weighs only half as much as *B. quadridentatus* (periphytic), although both have an almost identical habitus and shape. The same holds true for the periphytic *Euchlanis dilatata*, the phytophilous *Testidunella patina* and sessile forms like *Stephanoceros fimbriatus* and *Floscularia ringens* (Table 8). The limnetic *Brachionus calyciflorus* is another light-weight species, but *Filinia longiseta* is rather heavy. However, its buoyancy is increased by its 3 long appendages. *Polyarthra* and *Hexarthra* are also relatively heavy limnetic species, but they have a strongly developed muscle-system and are probably good swimmers.

The only comparable rotifer data in the literature are on *Keratella quadrata* (O.F.M.) (Doohan and Rainbow, 1971). The weight found by these authors, is much lower than ours, being more in the range of our *Keratella cochlearis.*

As far as egg-weights are concerned, finally, data for some *Brachionus*-species were collected. Depoortere and Magis (1967) give a mean dry weight of 0.04 μg for an egg of *Brachionus leydigi*. Our figure for the slightly larger *B. angularis,* 0.07 μg, is well comparable to that.

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