

A review of some problems in zooplankton production studies

H. H. BOTTRELL, A. DUNCAN, Z. M. GLIWICZ, E. GRYGIEREK, A. HERZIG,
 A. HILLBRICHT-ILKOWSKA, H. KURASAWA, P. LARSSON &
 T. WEGLENSKA

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The problems associated with the measurements of the three main variables used in production estimates - standing crop, individual weights and development times - are reviewed within the context of attaining absolute comparisons between water bodies. The paper is mainly based on data collected during the International Biological Programme (IBP).

Howard H. Bottrell, Department of Zoology, University of Reading, Reading, U. K. Present address: Institute for Marine Environmental Research, 67 Citadel Road, Plymouth, U. K.

Annie Duncan, Department of Zoology, Royal Holloway College, University of London, Englefield Green, Surrey TW20 9TY, U. K.

Maciej Gliwicz, Department of Hydrobiology, University of Warsaw, Nowy Swiat 67, 00-046 Warsaw, Poland.

Eugenia Grygierek, Inland Fisheries Institute, 05-500 Piasczeno, Zabieniec, Poland. Alois Herzig, Limnological Institute, Austrian Academy of Sciences, Berggasse 18/19, A-1090 Vienna, Austria.

Anna Hillbricht-Ilkowska & Teresa Weglenska, Institute of Ecology, Polish Academy of Sciences, Dziekanow Lesny, near Warsaw, Poczta Lomianki, Poland. Hideo Kurasawa, Department of Biology, Shinshu University, Matsumoto, Nagano-ken, Japan.

Petter Larsson, Zoological Museum, University of Oslo, Sars gate 1, Oslo 5, Norway.

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INTRODUCTION

The number of individuals present, their individual weights and development times are basic variables. Each can be measured directly and used in estimating biomass and production. Thus a knowledge of the accuracy and comparability of these basic parameters is essential if estimates of biomass and production are to be accurate and comparable. Although there has been a large volume of work within the International Biological Programme, section dealing with the production of freshwaters (IBP/PF), such basic problems as accuracy, precision and comparability still remain largely unresolved. In the absence of comparable data there exists little

possibility of generalizing on the structure and function of the planktonic system, or on the greater problem of a general theory of biological productivity. Production is the product of a number of individual and population processes, so that all the problems of accuracy and comparability encountered with the basic parameters are magnified.

The aim of this review is to consider the problems associated with the estimation of standing crop, individual weights and development times within the context of attaining comparable values of biomass and production for different water bodies. In addition to providing the possibility of making past and future data comparable, a review of the IBP/PF zooplankton data will enable the main sources of error and the major gaps in our knowledge to be identified, and cooperative research to be initiated in the areas most requiring further study. The outcome of our efforts relies to a certain extent on the availability of raw data from a wide range of freshwater habitats. It is only with raw data that the data's accuracy, precision and comparability can be assessed properly. Accuracy and precision are used as defined by Sokal & Rohlf (1969): 'accuracy is the closeness of a measured or computed value to its true value; precision is the closeness of repeated measurements of the same quantity'.

This paper is largely based upon IBP/PF results from Data Reports and upon communications from IBP zooplankton workers. It is not intended as a summary of IBP zooplankton studies which the reader can find in Nauwerck (in press).

The IBP/PF Handbook No. 17, edited by Edmondson & Winberg (1971), was written at the beginning of IBP and gives a comprehensive introduction on how to measure the basic variables for estimation of production, but only to a minor extent is the accuracy and precision of different methodology considered. No attempt has been made to deal with this problem in the IBP Summary Volumes, despite its relevance to comparability, which is the heart of the Programme.

Most experienced plankton workers have considered these questions for their own organisms but may be content with achieving good relative estimates of density. Comparability of absolute values, both for the same organism and across different taxonomic

groups (plants, bacteria and animals) is a less frequent aim and is an essential requirement in ecosystem studies exploring ecologically significant biological interactions. How few IBP projects considered this whole problem was revealed in the Data Reports. The extent to which IBP underestimated the importance of obtaining absolute values with confidence limits as well as the time needed for analysis both during and at the end of the Programme will be revealed in the Summary Volumes when they appear. This paper originated out of the impossibility of handling other people's raw data except collaboratively and of comparison of absolute values except when based upon raw data handled cooperatively: this was the experience of a group of zooplankton workers investigating different water bodies in all of which ecologically significant interactions occurred between animals and plants and/or bacteria.

STANDING CROP

The abundance of zooplankton in freshwaters is continuously changing in space and time. This spatial and temporal variability makes it difficult to estimate abundance from samples which are also separated in space and time. The number of individuals is the most commonly used measure of standing crop from which population biomass and production are calculated. However, direct measurements of biomass by weighing and chemical determination have also been used routinely. These methods have some of the same problems as density estimates but only numbers will be considered here.

The spatial and temporal changes in density, the different efficiencies of various collecting gear and the time involved in sampling and processing must all be taken into account in devising an optimum sampling and processing strategy. The aim of a sampling strategy should be how to obtain the most unbiased estimate of adequate precision of mean density and of deviations about the mean density commensurate with an acceptable counting load, yet retaining the possibility of comparison between different water bodies. Since zooplankton workers have tended to solve their methodological problems in a way which suits their own situation,

many techniques and strategies for estimating zooplankton abundance have been used in IBP projects so that comparison between projects are difficult. However, relative comparability has been achieved by adopting a similar procedure for several water bodies with a single project. Although it is impossible to have a standard strategy to cover all water bodies, comparability can be achieved if the relative efficiency of various samplers is known under a range of sampling conditions in each water body, and density estimates adjusted to the most efficient sampler; the most efficient sampler being the one which catches the greatest number of individuals. The most efficient sampler need not necessarily be the sampler used in routine sampling. Selection of the routine sampler and the determination of its efficiency is only part of the problem. The extent to

which such comparisons are valid depends not only on the efficiency of the collecting gear, but also on the whole procedure of collection, examination and analysis. These will be examined in the following sections.

Collection

Concentration of zooplankton. — There are two ways of concentrating zooplankton from water samples: by sedimentation, and by filtration through netting. The former is the only satisfactory way to concentrate planktonic protozoans and is the best method for rotifers but is practical only at high densities. Filtration is by far the commonest method. In the Data Reports, 30 projects have provided information on the mesh size of the netting used: five projects have used mesh sizes of 40 µm or smaller, 10 used 41–50 µm, two used 51–60 µm, eight used 61–70 µm and

TABLE I

A comparison of the numbers of adult rotifers concentrated by sedimentation and by filtration through nylon netting of 70 µm mesh size (Ejsmont-Karabinova, unpubl.).

- S : the numbers of rotifers in a sedimented sample.
 C : the numbers of rotifers retained by and washed off the netting material^x. This is normally the only fraction which is counted.
 F : the numbers of rotifers passing through the net mesh into the filtrate^x.
 S-C-F : the calculated remainder. These are rotifers probably adhering to the netting material.
 x : in a filtered sample.

Species	Length (µm)	Sedimented numbers (ind./l.)	Percentage of numbers sedimented		
			Filtered C	In filtrate F	Remainder S-C-F
Anuraeopsis fissa	60	71	38	55	7
Polyarthra minor	80	2344	65	30	5
Polyarthra dolichoptera	120	457	70	6	24
Polyarthra vulgaris	120	15 239 853	47 56 71	20 10 6	33 34 23
Keratella cochlearis	130-195	90 546 4494	70 90 94	23 10 0.5	7 0 5.5
Keratella quadrata	146-370	12 240	39 87	2 1	59 2
Kellicottia longispina	515-832	10 26 163	97 46 84	3 0 1	0 54 15

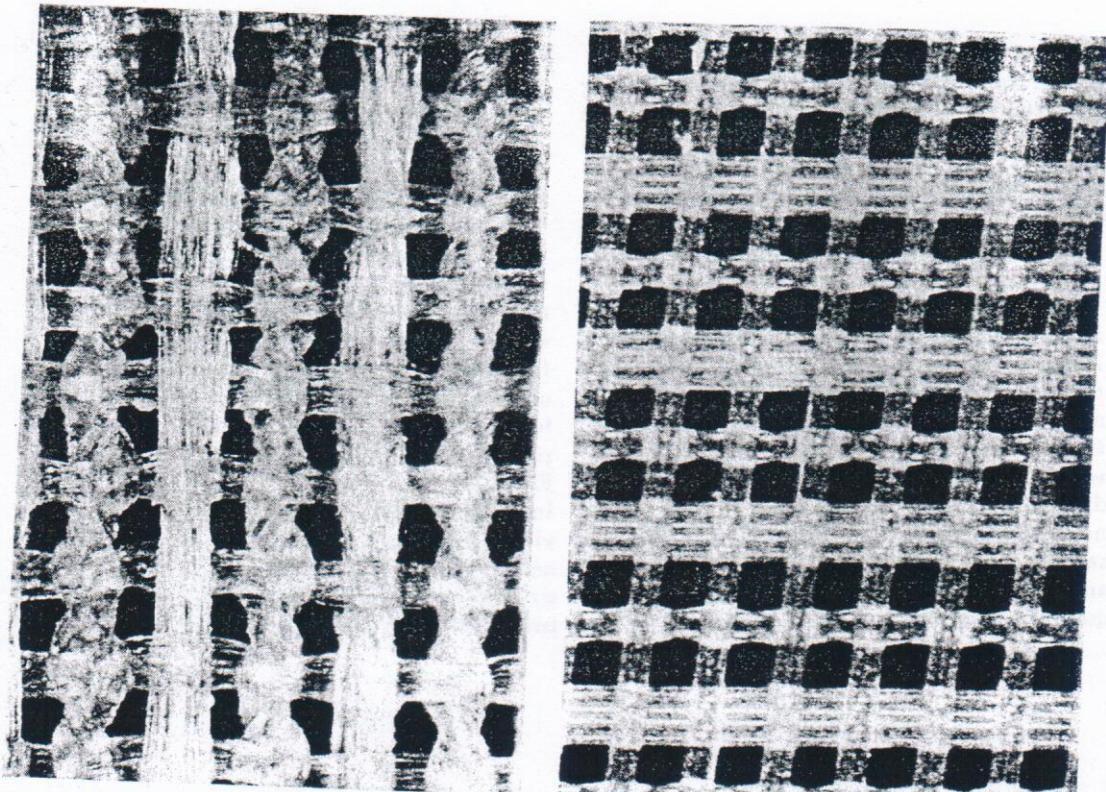


Fig. 1. Netting of the same mesh width: (a) from silk; (b) from nylon.

five used mesh larger than 70 μm . Those using the largest mesh sizes dealt only with Crustacea.

Hitherto, it has been believed that a 65–70 μm mesh collects rotifers sufficient for quantitative purposes, but the following observations demonstrate that this is not true for the smaller rotifers. Doohan (1973) compared the number of rotifers in sedimented samples and in samples filtered through a 65 μm mesh and found that only 40% of the rotifers such as *Keratella quadrata* were retained by the net. In Øvre Heimdalsvatn, Norway, the efficiency of different mesh sizes in collecting rotifers was compared (Larsson, in manus.). *Kellicottia longispina* was retained to the same degree by nylon netting with mesh sizes of 65, 45 and 20 μm , whereas *Polyarthra vulgaris* was slightly underestimated by filtration through 65 and 45 μm compared with 20 μm . This agrees with the published results of Likens & Gilbert (1970), which show that the soft-bodied *Polyarthra vulgaris* may pass

through mesh sizes of 75 and 48 μm but are retained on a 35 μm mesh; on the other hand, the loricate *Keratella cochlearis* remained on all three mesh sizes.

In addition to the loss of smaller rotifers, there are errors associated with concentration by filtering through netting, namely improved retention with increased densities and the adherence of certain rotifer species to the mesh. An example of improved retention is given for *Polyarthra vulgaris* and *Keratella cochlearis* in Table I (see column C), which presents the unpublished results of Ejsmont-Karabinowa. An appreciable clear size selection is also demonstrated since 35–55% of the rotifers smaller than 80 μm and up to 20% of those larger than 120 μm were not retained by the 70 μm mesh. There was no difference between loose eggs and adults apart from *Anuraeopsis fissa* with eggs which were caught more efficiently than those without eggs, probably because of their greater width.

TABLE II

Size of randomly selected meshes in silk and nylon netting (FBA) with 180 meshes per inch.
 h = height of mesh; w = width of mesh;
 \bar{X} = mean length of μm ; SD = standard deviation.

Netting type	Measurement	\bar{X}	SD
Silk	h	65.9	10.5
Silk	w	82.6	10.6
Nylon	h	68.5	3.4
Nylon	w	67.5	4.2

Another aspect of the filtration process that needs consideration, is the variability of the mesh size in the same sheet of netting. In general, nylon netting has a less variable mesh size than bolting silk (Fig. 1 and Table II). See also Tranter & Smith (1968). Table III presents the unpublished results of Hillbricht-Ilkowska for the number of rotifers retained by bolting silk compared with samples in which rotifers were sedimented. Although of smaller mesh size than that used

by Ejsmont-Karabinowa the filtering efficiency of the bolting silk is less good, probably because of the greater variability of its mesh size. Only 20% of the small *Trichocerca roussetti* and 40% of the larger *Synchaeta kitina* were retained. Species larger than 100 μm were retained most efficiently but so were species such as *Kellicottia* which seemed to stick to the silk. The loss through nylon netting was high because Ejsmont-Karabinowa used a relatively large mesh size for small rotifers.

Table III also shows the high losses due to the adherence of rotifers to the net material, but this loss is probably affected by the construction of the filtering unit and variability in the rinsing process. Although these results concern rotifers the problems discussed also apply to crustaceans. However, little is known concerning the degree of underestimation caused by the passage of nauplii through different mesh sizes and the adherence of crustaceans to the netting.

Collecting gear. — The variability of physical and biological characteristics of the water bodies studied has enforced the use of different collecting gear. Of the 38 IBP projects

TABLE III

A comparison of the numbers of selected rotifers concentrated by sedimentation and by filtration through silk netting of 45 μm mesh size (Hillbricht-Ilkowska, unpubl.).

- S : the numbers of rotifers in a sedimented sample.
 C : the numbers of rotifers retained by and washed off the netting material in a filtered sample. This is normally the only fraction which is counted.
 F : the numbers of rotifers passing through the net mesh into the filtrate in a filtered sample.
 S-C-F : the calculated remainder. These are the rotifers probably adhering to the netting material.

Species	Length (μm)	Sedimented numbers (ind./l.)	Percentage of numbers sedimented		
			Filtered C	In filtrate F	Remainder S-C-F
<i>Trichocerca rousseleti</i>	80	246	21	50	29
<i>Synchaeta kitina</i>	100	190	42	20	38
<i>Keratella cochlearis</i>	150	718	97	1	2
<i>Kellicottia longispina</i>	500	84	80	1	19
<i>Trichocerca</i> sp.	280	8	25	10	65

TABLE IV

A comparison of the efficiency of various volume samplers. Values are the mean \pm standard deviation in numbers per litre (Larsson, in prep.).

Species	Sampler			
	Schindler	Hand pump	Friedinger	Ruttner
<i>Kellicottia longispina</i>	4.33 \pm 1.32	7.40 \pm 2.96	10.23 \pm 3.21	9.67 \pm 4.08
<i>Polyarthra vulgaris</i>	11.30 \pm 3.11	12.75 \pm 5.15	18.29 \pm 3.55	19.33 \pm 4.37
<i>Bosmina longispina</i>	1.07 \pm 0.50	3.05 \pm 1.12	2.49 \pm 1.26	2.40 \pm 1.51
<i>Holopedium gibberum</i>	0.52 \pm 0.26	0.80 \pm 0.59	0.98 \pm 0.59	0.79 \pm 0.68
<i>Cyclops nauplii</i>	4.48 \pm 0.71	2.25 \pm 1.53	2.96 \pm 1.13	3.33 \pm 1.51
<i>Cyclops copepodites</i>	11.97 \pm 2.50	6.50 \pm 3.54	11.09 \pm 2.28	9.60 \pm 4.12

containing information about their sampling equipment, 20 used vertically hauled nets, two used horizontally towed net samplers with a built-in flow meter (e.g. Clarke-Bumpus and Isaacs Kidd high speed sampler), 13 used some kind of volume sampler and six used pumps which are a form of volume sampler. Only three projects mentioned the use of more than one type of collecting apparatus for routine quantitative sampling.

Plankton samplers can be divided into two basic types: net samplers which simultaneously collect and concentrate the zooplankton, and volume samplers in which a known volume of water has to be filtered after collection to concentrate the zooplankton.

Volume samplers were probably the most accurate in that usually they gave the highest densities. Comparisons carried out by Langeland & Rognerud (1974) and Larsson (in manus.) show that in general volume samplers are very similar in the level of their catching efficiency (Table IV), but that they may differ in their efficiency of capture of fast swimmers with good sense organs. The properties of the samplers which are relevant to obtaining reliable density estimates are that they close quickly and cause minimal response by the organisms (Szilauer 1964, Smyly 1968, Schindler 1969, George 1972). Pumps, which are a special form of volume sampler, are basically of two types. The motorized pump

with its continuous flow has a greater efficiency of capture, and is to be preferred to the hand pump. A motorized pump with a transparent intake tube was used routinely in the River Thames and, besides being the only practical method, gave the highest densities compared with an opaque Patalas sampler and a net, which caught 70% and 30% respectively of the total zooplankton (Bottrell, in prep.). The use of pumps compared with the conventional volume samplers needs to be tested in the future, particularly with respect to the type of pump, their rate of flow, the suction pressure, the intake tube visibility, species response and the effect of water movement past the intake tube.

Nets with an attached flow meter behave like volume samplers but possess the additional advantages of being able to collect large and integrated samples and having been well studied. However, the most widespread collecting tool, even for quantitative sampling, was a vertical net haul without a flow meter. Without a flow meter the amount of water filtered during a net haul is unknown but will always be less than the cross-sectional area of the net opening multiplied by the length of tow. Most estimates, however, were based upon the assumption that the water filtered is equal to the volume of this column. This provided relative estimates which were internally consistent but incom-

TABLE V

Linear regressions relating numbers of individuals per vertical net haul to numbers of individuals per Patalas depth-series when sampled simultaneously and at weekly intervals throughout one year (based on T.E. Andrew's data for Queen Mary reservoir, England, collected during 1968-69).

cl = confidence limits; df = degrees of freedom; F = variance ratio; P = level of significance; regression equation: $\ln N = a + b \ln P$, where N represents the number of individuals in five 5-litre Patalas samples distributed throughout the depth and filtered through the same mesh of netting. The net hauls were sub-sampled whereas the Patalas samples were counted totally.

Species	$\ln a$	$b \pm 95\% cl$	df	F	Net loss factor $P \cdot \frac{847}{N \cdot 25}$
Daphnia hyalina	2.437	0.966 ± 1.430	1;45	178	3.4
Cyclops vicinus	2.870	0.902 ± 0.217	1;35	66	2.6
Diaptomus gracilis	1.832	1.101 ± 0.342	1;36	40	4.3

parable with other work. Comparisons have been made between nets and volume samplers, all of which have demonstrated that nets generally collect less than traps per unit volume (Patalas 1954, Karabin 1971, Duncan 1975a, b). The results of Patalas (1954) show that in a stratified Polish lake a volume sampler of his own construction gave densities of total zooplankton up to 2.56 times nets. Karabin (1971) found that the density of *Leptodora kindtii* was up to eight times larger in the volume sampler than in the net hauls.

In the London reservoirs two approaches were adopted for calibrating vertical net hauls with volume samplers taken as a depth series with a 5 litre Patalas sampler. In one approach, replicate samples of both collecting methods were taken under calm weather conditions and revealed that a 'net-loss' factor of 2.7 (with 95% confidence limits of 1.9-3.7) was needed to equate net biomass or numbers to Patalas values. In a second approach, the routine weekly net and Patalas samples, collected by both methods under the normal annual range of collecting conditions, provided numerical data for separate species from which regressions relating the two methods were calculated. These regressions are given in Table V. The net-loss factors derived from these regressions fell with-

in the confidence limits of the one mentioned above apart from that for *Diaptomus*, which was higher. For the purpose of absolute comparisons between water bodies, the validity of correction factors for collecting gear has to be established, particularly with respect to their variation within and between lakes, between species, between night and day samples, care of rinsing and individual net structure.

Collecting stations or positions. — The points at which samples are collected should be determined by the distribution of the plankton in the water body. As no *a priori* knowledge of plankton distribution of a particular day is available, a decision has to be made on the vertical and horizontal points in the water body from where samples are to be taken. There is no information in the Data Reports on how this decision was taken and whether random, systematic or stratified sampling was chosen. Despite discussions of this problem by Cassie (Edmondson & Winberg 1971), and others, IBP zooplankton workers have found sampling theory difficult to implement when dealing with whole water bodies and, intuitively, have probably adopted some form of systematic sampling vertically and horizontally. In addition to vertical and hori-

TABLE VI

The mean density and confidence limits of zooplankton in various IBP water bodies. Mean and 95% confidence limits as percentage of mean. All numbers transformed to natural logarithms.

Water body	Date	n	Cyclops scutifer, copepodites + adults	Cyclops scutifer, nauplii	Bosmina longispina	Kellicottia longispina
1. Ø. Heimdalsvatn Norway	30.07.69	130	*	2.253 ± 5.78	1.022 ± 19.63	2.583 ± 4.32
	10.08.69	130	*	1.259 ± 23.65	3.108 ± 26.52	2.668 ± 6.97
	26.08.69	132	1.694 ± 11.73	1.802 ± 9.13	1.964 ± 10.07	3.134 ± 2.93
	10.09.69	134	2.016 ± 6.21	*	2.385 ± 7.26	3.102 ± 2.45
2. Loch Leven Scotland	23.03.69	66	3.159 ± 3.78	4.543 ± 2.45		
	17.04.69	68	4.449 ± 4.45	3.077 ± 5.78		
	07.05.69	68	4.775 ± 2.15	4.359 ± 1.86		
	07.06.69	68	5.326 ± 1.51	5.946 ± 3.33		
	08.07.69	68	6.114 ± 1.58	4.705 ± 1.48		
	08.08.69	68	5.648 ± 2.55	3.516 ± 6.11		
	29.08.69	68	5.162 ± 3.78	4.967 ± 5.09		
	01.10.69	68	5.382 ± 1.80	4.099 ± 0.83		
	22.10.69	68	5.071 ± 2.05	2.053 ± 3.62		
3. Lake George Uganda	19.12.68	20	Total zooplankton	Total Copepoda	Total Cladocera	Total Rotifera
	03.04.69	20	6.788 ± 2.49	6.124 ± 4.36	4.003 ± 8.20	5.768 ± 3.61
	14.05.69	20	6.455 ± 2.90			
	26.06.69	20	6.428 ± 3.25			
	05.06.69	20	6.377 ± 2.08			
	15.09.69	20	6.796 ± 2.02			
	27.10.69	20	7.141 ± 3.95			
	09.12.69	20	6.628 ± 3.90			
	21.01.70	20	6.475 ± 5.29			
	02.03.70	20	6.412 ± 3.33			
	13.04.70	20	6.652 ± 3.19			
			6.573 ± 3.93			
4. River Thames (above R. Kennet) England	26.01.71	48	Total zooplankton	Diaptomus gracilis nauplii	Bosmina calyciflorus	Asplanchna priodonta
	24.02.71	48	2.949 ± 1.41	2.771 ± 0.59		
	21.04.71	48	2.459 ± 4.08	2.360 ± 1.59		
	19.05.71	48	3.650 ± 0.45	2.145 ± 0.80	3.600 ± 1.04	1.401 ± 55.9
		48	4.793 ± 0.10	3.430 ± 1.14	4.136 ± 0.25	2.105 ± 9.0
5. Queen Elizabeth II reservoir, England	19.01.71	49	Total zooplankton	Leptodora kindtii ^a	Cladocera	Copepoda
	05.07.71	20	4.816 ± 1.65	3.301 ± 9.27		
					4.390 ± 0.1	2.690 ± 6.6
6. Zabieniec fish ponds, Poland	09.06.70	34	Total zooplankton	Total zooplankton	Total zooplankton	
	06-08.07.71	74	pond 34 2500 fish per ha	pond 39 7500 fish per ha	pond 40 No fish	
7. Jezioro Mikolajskie Poland	12.07.61	20	Total zooplankton	Cladocera	Copepoda	Rotifera
	05.08.61	20	5.515 ± 3.05	4.764 ± 3.08	5.032 ± 19.80	7.036 ± 4.97
	20.10.61	10	5.746 ± 1.91	5.189 ± 3.30	5.606 ± 7.58	7.755 ± 2.47
			3.096 ± 8.89	5.396 ± 4.57	5.630 ± 4.79	7.370 ± 2.89
	15.05.64	15	Total zooplankton	Cladocera	Copepoda	Rotifera
	28.07.64	16	7.367 ± 4.73	6.391 ± 3.93	5.032 ± 19.80	7.036 ± 4.97
			8.199 ± 2.30	5.4	5.606 ± 7.58	7.755 ± 2.47
	22.08.64	16	7.043 ± 2.42	5.464 ± 4.01	5.630 ± 4.79	7.370 ± 2.89
	09.09.64	16	7.120 ± 2.35	5.420 ± 2.06	5.152 ± 3.98	6.496 ± 2.47

^a zero counts present

x n = 11

- P. Larsson (unpublished). 2.57-litre Friedländer sampler; 8 stations with depth samples at 1 m intervals; 5-13 depths; 2 replicates; numbers per 2.57 litres.
- A. Walker (1970). 5-litre transparent sampler; 8 stations; 1-3 depths; 2 replicates; numbers per 5 litres.
- M.J. Burgis (1971). Integrated column sample by tube; 20 stations; numbers per litre.
- H.H. Bottrell (in prep.). Pump samples; River Thames: 3 stations; 4 depths; 4 replicates. River Kennet: 1 station; 3 depths; 4 replicates; numbers per m³.
- A. Duncan (unpublished). Integrated column sample by vertical net haul from 1 m above the bottom to surface; 20-37 stations; 2 replicates; mg dry weight per haul; Cladocera and Copepoda separated by narcotization and shaking.
- E. Grygierek (unpublished). 1-litre Patlanus sampler; 20 stations; 1 depth; numbers per litre.
- Chojnicka, Hillbricht-Ilkowska (unpublished). 5-litre volume sampler; 16 stations; 3 depths (1m, 3m, 6m) bulked before counting; numbers per 3 litres.

zontal variability a further source of error is the replicability of samples at one point. Ideally these three sources of error will be assessed before a final decision is made.

This can be done using an analysis of variance to partition the total variance between these three effects, but demands adequate point sampling and an orthogonal design for the analysis. However, because of the uneven depth of many water bodies, the number of depths from which samples are collected may not be the same for each surface station. This results in a multiway analysis of variance with unequal, and usually disproportionate, subclass sizes, that is, the analysis is no longer orthogonal. This means that the sums of squares of the effects do not add up to the total sums of squares since the separate effects are not independent, and therefore cannot be separated completely. Because of the ambiguity of interpretation and the complexity of calculations, such a non-orthogonal analysis is not attempted in this paper.

The analysis may be made orthogonal by considering the common depths only or by summing the depth samples. This is not satisfactory as it involves loss of information and reduction of variance, and again it is not possible to separate the effects of horizontal and vertical position completely. In the water bodies for which this has been attempted, the variance associated with replicate samples was relatively small, whereas the variance associated with the vertical and horizontal position taken together was higher. The relative importance of the horizontal and vertical components is thought to be related to the pattern of water movement, the morphology of the particular water body, and the seasonal biology of the organism. In the River Thames at Reading an orthogonal design was possible since the depth of the main channel was more or less uniform. The analysis of variance gave non-significant values of the variance ratio for depth and position across the river, from which it was inferred that the pattern of water movement produces a homogeneous plankton distribution (Bottrell 1976).

Thus for analytical and practical reasons it is often difficult to partition the variance between the three sources of error. However, a composite measure of these errors is given

by fitting 95% confidence limits to the mean for the whole water body. Table VI shows that these confidence limits are often less than 10% of the transformed mean. In those water bodies where only one depth has been sampled (Zabieniec; Lake Mikolajskie), or where an integrated column sample was taken (Lake George, Uganda; the London reservoirs), the low confidence limits reflect horizontal homogeneity of distribution. In Øvre Heimdalvatn, where a large number of point samples were taken routinely, heterogeneity in the vertical distribution of *Bosmina longispina* resulted in confidence limits wider than $\pm 10\%$ on several occasions. Such vertical heterogeneity is not revealed in the other sites with extensive point sampling (Loch Leven; River Thames; River Kennet), all of which appear to be well mixed horizontally and vertically. According to Smith (1974) complete mixing can be assumed for Loch Leven so that a single sample is usually representative of the loch as a whole. Whether or not the level of vertical heterogeneity found in Øvre Heimdalvatn is usual for zooplankton from less well-mixed lakes and reservoirs has to await results on the total variance from point sampling. The validation of Table VI as a comparison of absolute densities awaits clarification about the nature of the sampling in the water bodies cited. This requires the aid of a biological statistician and a comparison of numerical data from well-mixed plankton sampled randomly and systematically.

Examination

Counting. — The examination of samples involves counting a small sample totally, or a subsample from a large one. There is some variability associated with different counters, but this is low as is shown by the results from Øvre Heimdalvatn (Larsson, in manus.), where 29 replicate samples taken from one station were counted by two experienced counters. Results from paired counts of each replicate showed that the difference between counters was negligible, that is, the two counters worked with high precision.

Subsampling. — In more than half of the IBP projects it was necessary to subsample to reduce counting effort. Subsampling intro-

duces a new source of variability into the estimates of mean density which must be quantified. Initially, it is necessary to check that a random distribution exists within the shaken sample bottle from which subsamples are to be taken by plotting the mean number per subsample (\bar{x}) against the variance (S^2) for samples of a wide range of densities; $S^2 = (\bar{x})$ indicates a random distribution and agreement with a Poisson distribution. Several authors have reported checking their subsampling technique (Kott 1953, Venrick 1971, Ekbohn & Dottne-Lindgren 1973, Langeland & Rognrud 1974). Although several subsampling techniques for zooplankton have been described (Edmondson & Winberg 1971), and some have been compared (Rybäk 1960), the commonly adopted method in IBP zooplankton studies involved taking subsamples of known volume from a concentrated sample and doing a total subsample count. The instruments commonly used were either a calibrated wide bore tube with teat or the Hensen 'Stempel' pipette, which has a plunger shaped to enclose a definite volume when it is drawn up into the bore of the tube. The volumes most commonly counted using these subsamplers were 2.5 ml and 5.0 ml. Alternatively a calibrated wide bore tube may be used to dispense a series of 5–10 drops of about 1 ml each (the 'drop' method) into a class slide for counting. Tests on the efficiency of these two subsamplers used in these two ways show that in both the coefficient of variation decreases with increased density

per subsample (Fig. 2). Above a mean density of 50–60 individuals per 5 ml subsample with a Stempel pipette, the coefficient of variation becomes stabilized within the 2–8% range, whereas the level at which this happens in the drop method is at a density of 10–15 individuals per 0.1 ml drop, above which the coefficient of variation becomes stabilized around 20%. The advantage of the drop method is that it involves less handling of small-bodied zooplankton, particularly with regard to their identification under high magnification. Subsamplers of other types also possess their own characteristic sources of bias and variability but little information on these are available. The Motoda splitter (Motoda 1959) when used carefully can produce good results with small-bodied zooplankton but is less convenient as it involves more handling than the wide bore tube and Stempel pipette.

Analysis

Neither adequate statistical analysis nor the raw data were available in the zooplankton IBP Data Reports, although the basic analytical techniques are well documented in statistical handbooks (Snedecor & Cochran 1967, Sokal & Rohlf 1969, Elliott 1971, Gilbert 1973). Only by using the basic approach outlined below was it possible to produce the comparative tables (Tables VI, VIII, X, XII, XIII) presented in this paper.

Mean, variance and transformation. – If the aim of an investigation is to obtain a good estimate of mean density on each sampling occasion, then it seems expedient also to make an estimate of the precision of the mean. The latter requires that samples are replicated. The factor limiting the degree of replication is not generally the time involved in collecting the samples but the time it takes to count the samples. The number of samples that can be counted relative to the number it is statistically desirable to count is usually low, and this has considerable practical implications for the statistical analysis of the data.

The low number of samples collected on any one sampling day at any one sampling position make it difficult to define the statistical distribution of the counts in the samples. The normal distribution is rarely

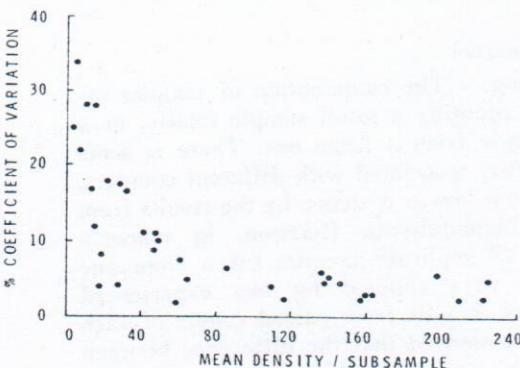


Fig. 2. Relationship between the coefficient of variation and the mean density of *Daphnia* per subsample, using a 5-ml Stempel pipette (George 1972).

a suitable model for counts, but it is important because many statistical methods (for example, correlation coefficient, significance tests, analysis of variance) demand that the data follow a normal distribution. Thus it is usually necessary to transform the counts in order that the data will follow approximately a normal distribution.

If the original distribution is unknown because there are too few samples, then the choice of which transformation is used may be based on the relationship between the variance and the arithmetic mean (see Elliott 1971). Since the variance is often considerably larger, and positively correlated with the mean in plankton sample counts, a logarithmic transformation is generally the most applicable. The logarithmic transformation has the added advantages that it not only makes the data approximately normally distributed, but also reduces the variance, gives homogeneity of residual variances, and additivity of the components of the variance. The adequacy of a transformation is tested by determining if the transformed variance is independent of the transformed mean. All subsequent calculations such as, analysis of variance, regression analysis and fitting of 95% confidence limits should be carried out using the transformed data.

Variance of bulked samples. — In some water bodies, e.g. Øvre Heimdalsvatn, a large number of point samples may be the only strategy suitable for obtaining a realistic estimate of mean density. If it is not feasible to count a large number of samples routinely then the counting load may be reduced by bulking. The way in which the samples are bulked does not affect the estimate of mean density, but can greatly affect the estimate of the variance of the mean.

Consider a lake in which the greatest variation in density occurs along its long axis, and in which four samples are taken in each of the four zones of different density (Fig. 3a). The best unbiased estimate of the variance of mean density for the whole lake is given by using all 16 samples, assuming these samples to be independent; best being used in the sense of minimum variance of the estimated variance. If the expected value of the density in the i^{th} group differs from μ by a quantity B_i , then the variance estimate

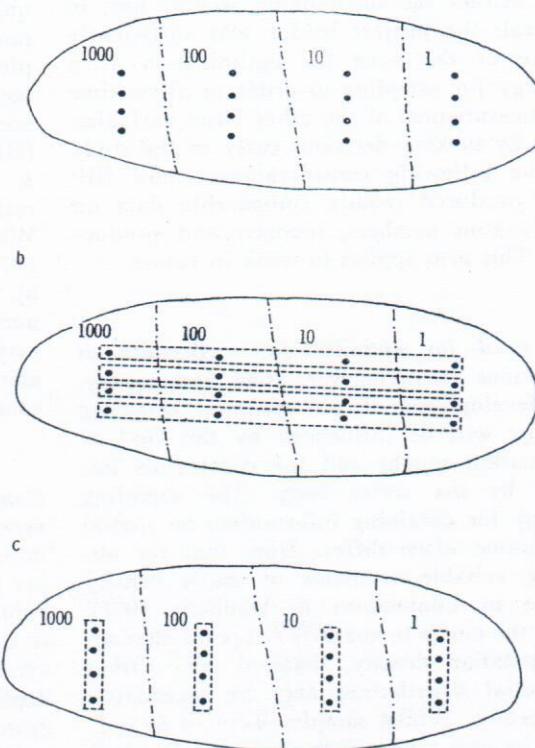


Fig. 3. Variance of bulked samples; numbers are densities in each zone, • represents a sample, - - - indicates boundary between density zones, - - - - indicates the direction in which the samples were bulked.

obtained from the groups will be equal to the variance of the mean density plus a function of B_i . If bulking has to take place and the groups are chosen such that $B_i = 0$ for all i , the variance estimate will be unbiased; this will be the case if samples are bulked along the long axis (Fig. 3b). However, if the groups are chosen such that $B_i \neq 0$ for all i , the variance estimate will be biased; this will be the case if samples within each density zone are bulked (Fig. 3c). Therefore, as a general rule bulking should take place along the axis of greatest variation in density.

Strategies

Logistic problems arising out of the need for representative sampling when the aim is estimation of total numbers is discussed by Cassie (in Edmondson & Winberg 1971). These problems were magnified in IBP pro-

jects which required information about zooplankton biomass and production. It is clear that neither the zooplankton worker nor, in general, the project leader was sufficiently aware of the need for optimization as a strategy for sampling in order to allow time for measurement of the other basic variables. Only by making decisions early in the study on the following considerations could IBP have produced readily comparable data on zooplankton numbers, biomass and production. This also applies to work in future.

The need for optimization. — Because of limitations in manpower, time and money, the development of an optimum sampling strategy will be influenced by the kind of information sought and the constraints imposed by the water body. The sampling strategy for obtaining information on spatial distribution often differs from that for obtaining reliable estimates of mean density (Cassie in Edmondson & Winberg 1971). When the aim is to quantify temporal changes in population density, detailed information on spatial distribution may be considered unnecessary. Whilst samples have to be collected in such a way as to cover vertical and horizontal distribution, both the counting load and the variance of the mean may be reduced by collecting integrated large volume samples or by bulking many small volume samples. In most water bodies, some degree of integration or bulking will almost certainly be necessary if adequate estimates of population density are to be obtained within the limits set by the maximum possible counting load. All samples, whether integrated *in situ* or bulked after collection should be replicated. The main axis of integration will be dictated in most cases by the physical characteristics of the water body; depth and area being the main consideration in lakes, while in rivers flow must be taken into account.

However, because of the nature of the energy input into aquatic ecosystems the depth component is of fundamental importance. Investigations which require information on vertical distribution of population density and structure for use in calculating depth variable rates may find integration along the horizontal axis to be a desirable com-

promise which allows some reduction of counting load while also retaining the required vertical information. Another important consideration is the necessity to sample planktonic organisms just above the bottom (Smyly 1974) and within the sediments which may provide food for nauplii (Gliwicz 1967) or Cladocera (Nadin-Hurley & Duncan 1976) or shelter for copepod resting stages (Smyly 1961, Elgmork 1959, Wierzbicka 1962, Edmondson & Winberg 1971) or cladoceran ephippia (Duncan 1975a, b). Without such samples the zooplankton numbers or biomass per unit surface area may be underestimated (Elgmork 1967, Edmondson & Winberg 1971, Darlington, pers. comm.).

Conversions to unit volume and unit surface area. — For the purpose of comparison, it is desirable that raw data be converted to values per m^2 of surface area and per m^3 . Since the volume of water present at different depths is not the same in most water bodies, conversion to m^2 or m^3 must be weighted by a depth factor. One consideration against integrated sampling is the impossibility of weighting with a depth or area factor the conversion of density per unit volume to density per unit surface area which is representative of the whole water body. Readers are referred to Hrbáček (1966) and Brandl (1973) for some discussion of the methodology involved. Larsson (1972) has considered the question whether distribution patterns are related to distance from the surface or from the bottom since this affects the way the depth factor can be applied. He concludes that in winter vertical distribution is related to distance from the surface but during the summer it was difficult to distinguish between the effects of distance from surface or distance from bottom. Rivers raise another problem of how meaningful is a density per m^2 of surface area or per m^3 in rapidly flowing water. It is possible to obtain two measures of density per unit volume: one representing an instant in time (numbers per m^3), the other representing a time-integrated density (numbers per m^3 per second). Unlike density per m^2 surface area, both of these measures are biologically meaningful. Numbers per m^3 are relevant to organisms floating

in the water whereas numbers per m^3 per second are more relevant to stationary organisms (Bottrell 1976).

Sampling strategies. — The choosing of the routine collecting tool or tools is influenced by various practical considerations in addition to its cost and efficiency of working. In shallow extensive lakes where vertical variation is poorly developed, as in Neusiedlersee (Herzig 1974), integrating samples towed horizontally will provide the most reliable population estimates. Whereas in a deep lake of relatively small surface area, where vertical variation is strongly developed, vertically towed integrating samplers will provide the most reliable estimate of mean density. In the case of a deep extensive lake (e.g. Lake Tanganyika) it will be necessary to integrate both vertically and horizontally, by sampling independently along both axes at the same time with oblique or undulating hauls. Such integrations, whether along the horizontal or vertical axis, or both, may be made with the least amount of sampling effort and cheaply by using low-speed towed nets or, more expensively, using high-speed oceanographic samplers such as the Isaacs Kidd or the Continuous Plankton Recorder (UNESCO 1968), or the Undulating Oceanographic Recorder (Bruce & Aiken 1975). Rivers are a special case where both depth and area are likely to be of lesser consideration than flow. Small shallow lakes of uneven depth (e.g. Øvre Heimdalsvatn) provide examples of water bodies in which neither adequate horizontal nor vertical integration can be made with integrating nets. In such water bodies samples have to be collected at numerous horizontal and vertical stations and bulked before further processing.

Before embarking on a long-term investigation, it is worth while spending some time testing the chosen, bought tool against as many other gear as can be borrowed, so that both its accuracy and precision have been defined. Usually this is done in good weather but it must be borne in mind that any tool works less efficiently when the collector is cold or wet and that its efficiency may vary with type and concentration of organisms.

Although a six-week sampling interval is acceptable in the dynamic steady-state system that seems to exist in the equatorial Lake

George, Uganda, the sampling interval in temperate and alpine water bodies needs to consider the generation time of the dominant organisms during their growing period. Ideally, sampling intervals should be less than the generation time, but weekly samples seem a reasonable compromise in temperate water bodies combined with longer sampling intervals at other periods of the year (Hillbricht-Ilkowska & Weglenska 1970). However, rotifers and protozoans should probably be sampled every few days when their life cycles are shorter than one week. The greater possibility of interpreting results compensates for the work involved in more frequent sampling.

INDIVIDUAL BODY WEIGHT

Every method of calculating secondary production requires a knowledge of the body size of zooplanktonic species at all stages in their life cycle. Size is also a factor influencing many rate processes significant in production ecology, such as respiration, excretion and feeding. The question of size in feeding has many facets since not only is the feeding rate size-dependent but the process also involves size selectivity which, furthermore, is influenced by the size of the consumer. Any comparison of the relative importance of different functional components within an ecosystem and between ecosystems must be based upon common units of measurement of biomass which, in animals, usually comes from numbers and body weights. Individual size is therefore a parameter of fundamental importance in ecosystem studies.

For production studies size as weight must be known although linear dimensions are more conveniently and immediately measurable during the process of counting. The most useful and commonly adopted measure of body size in IBP studies has been dry weight for planktonic crustaceans and rotifers but depends upon the availability of a good microbalance. For crustaceans where no balance is available, and for rotifers and protozoans, fresh weight has been obtained either by measuring volume directly by water displacement in small calibrated vessels (Pechen 1965) or from volumes computed from linear dimensions applied to simple

geometric shapes appropriate to the organism's body and assuming a density of 1.0 (from $10^6 \mu^3 = 1 \mu\text{g}$) (Lohmann 1908). Irregularly-shaped species are more difficult and several techniques have been tried; either the total volume can be obtained by summing the calculated volumes of a number of simple geometrical shapes fitted to the body (Osmera 1966), or by choosing an appropriate shape from a series of different shapes for which a length/fresh volume - weight has already been calculated (Chislenko 1968). Another approach was the construction of scale models of organisms and determining fresh weight by direct weighing or by measuring water displacement (Sebestyen 1955, 1958, Nauwerck 1963). Dumont et al. (1975) have pointed out that some of these procedures involve an accumulation of errors. Different procedures have different levels of error which may vary with species. The level of error is often not quantified, and is cumulated in production estimates.

Of the 51 IBP data reports containing information on zooplankton, only four mentioned protozoan sizes and only 15 gave rotifer sizes, mostly from computed volumes converted to fresh weight; in two reports dry weights were given for some species of rotifers. There was information in 24 reports on the sizes of crustaceans but not in the other 27, despite the fact that some results are given as fresh weight biomass. Where data on size were available, they were presented in various forms; as mg nitrogen (in four reports), as mean biomass per individual (in four), as wet weight converted from body volume (in 12) and as directly measured dry weight (in nine) or chemical content of protein, carbohydrates, fats, nitrogen, phosphate and chemical oxygen demand (in one). For some important species, length/weight regressions have been calculated, considerably adding to our stock of data on body size in zooplankton. Since the end of the IBP, another paper on dry weight estimates in a selection of Cladocera, Copepoda and Rotifera from plankton has been published by Dumont et al. (1975), which further expands our existing information.

The aim of this section is (1) to collate the size measurements of zooplanktonic animals used by IBP workers for calculating production, (2) to determine the comparability of

sizes for the same species obtained by different techniques and, where possible, to quantify the error, and (3) to assess how widely applicable are the available regressions of dry weight on length for different populations of a species or over a whole group (e.g. Cladocera or Copepoda).

Body size of Rotifera and Protozoa

Tables VII and VIII present the measured dry weights of five forms of Protozoa and 28 species, covering 16 genera, of Rotifera. Dumont et al. (1975) managed to weigh a sufficiently wide range of sizes in three rotifer species to calculate length/dry weight regressions which all possess low values for the slope. The weights for *Euchlanis dilatata* obtained by Bottrell (1975a) agree well with those recorded by Dumont et al. (1975), but the values for *Keratella quadrata* with and without eggs in Doohan & Rainbow (1971) and from Lake Suwa (Japanese IBP/PF) are much lower than those given by Dumont et al. (1975) and more similar to the weights for *Keratella cochlearis*. This seems to be a real difference since the value recorded by Doohan & Rainbow (1971) had 95% confidence limits of only $\pm 2.94\%$ of the mean and came from samples dried gently at room temperature over silica gel. Dumont et al. (1975) found no differences in the mean dry weights of *Asplanchna priodonta* weighed after being frozen, after 4 hours' fixation in 4% formaldehyde and after 9 years' preservation in 4% formaldehyde, whereas fixation in 70% ethanol resulted in loss in weight.

In most IBP reports, rotifer size was derived from volumes calculated using linear dimensions of either living or preserved animals applied to appropriate geometric shapes. Table IX lists the wet weights of

TABLE VII.

Linear regressions relating length (mm) and dry weight (μg) in freshwater Rotifera.

$$\text{Equation: } \ln W = \ln a + b \ln L$$

Species	$\ln a$	b
<i>Brachionus calyciflorus</i>	- 9.3348	1.44
<i>Euchlanis dilatata</i>	-12.1843	2.07
<i>Gastropus hyptopus</i>	- 8.5844	1.52

TABLE VIII. Individual body dry weights (μg) of freshwater Protozoa and Rotifera.

<u>Protozoa</u>	<u>Number</u>	<u>Mean weight</u>	
<i>Arcella vulgaris</i>		0.05	Lake Suwa, Japan. Japanese IEP-PF
<i>Paramecium</i> sp.		0.10	Lake Suwa
<i>Vorticella</i> sp.		0.025	Lake Suwa
<i>Tintinnidae</i>		0.013	Lake Suwa
<i>Carchesium polypinum</i>		0.013	Lake Suwa
<u>Rotifera</u>			
<i>Rotaria rotatoria</i>		0.20	Lake Suwa
<i>Brachionus urceolaris</i>	150,40,200	0.20,0.20,0.12	Sambre River, Belg. Dumont et al. (1975)
<i>B. calyciflorus</i>		0.11-0.47	Sambre River
<i>B. calyciflorus</i>		0.20	Lake Suwa, Japan. Japanese IEP-PF
<i>B. calyciflorus w. egg</i>		0.42	River Thames, G.B. Bottrell (1975a)
<i>B. angularis</i>		0.05	Lake Suwa, Japan. Japanese IEP-PF
<i>B. diversicornis</i>		0.15	Lake Suwa
<i>B. rubens</i>		0.15	Lake Suwa
<i>Keratella quadrata</i>	250,100	0.32,0.35	Univ.Pond, Gent, B. Dumont et al. (1975)
<i>K. quadrata</i>		0.07	Lake Suwa, Japan. Japanese IEP-PF
<i>K. quadrata w. egg</i>	450	0.143	London Res., G.B. Doohan & Rainbow (1971)
<i>K. quadrata w'out eggs</i>	5 x 90	0.075 *	London Res., G.B. Doohan & Rainbow (1971)
<i>K. cochlearis</i>		0.07	Lake Suwa, Japan. Japanese IEP-PF
<i>K. cochlearis</i>	350	0.11	Univ.Pond, Gent, B. Dumont et al. (1975)
<i>K. cochlearis</i>		0.037±0.003	ELA N.W.Ont. Can. Schindler & Novén (1971)
<i>K. valga</i>		0.07	Lake Suwa, Japan. Japanese IEP-PF
<i>Anuraeopsis fissa</i>		0.07	Lake Suwa
<i>Euchlanis dilatata</i>		0.30-1.00 **	Lake Donk, Belg. Dumont et al. (1975)
<i>E. dilatata</i>		0.50	River Thames, G.B. Bottrell (1975a)
<i>E. incisa</i>		0.30	River Thames, G.B. Bottrell (1975a)
<i>Trichocerca inermis</i>		0.10	Lake Suwa, Japan. Japanese IEP-PF
<i>Lecane</i> sp.		0.20	Lake Suwa
<i>Asplanchna priodonta</i>	400	0.525 ***	Pond, Gent, Belg. Dumont et al. (1975)
<i>A. priodonta</i>	150	0.487 ***	Lake, Gent, Belg. Dumont et al. (1975)
<i>A. priodonta</i>		0.44	Lake Suwa, Japan. Japanese IEP-PF
<i>A. brightwelli</i>		0.28-1.50 **	Rissani, Morocco. Dumont et al. (1975)
<i>Synchaeta oblonga</i>		0.022	London Res., G.B. Doohan (1973)
<i>S. stylata</i>		0.20	Lake Suwa, Japan. Japanese IEP-PF
<i>Synchaeta</i> sp.	200,200	0.27,0.26	Univ.Pond, Gent, B. Dumont et al. (1975)
<i>Ploesoma truncata</i>		0.10	Lake Suwa, Japan. Japanese IEP-PF
<i>Polyarthra vulgaris</i>		0.043	London Res., G.B. Doohan (1973)
<i>P. trigla</i>		0.20	Lake Suwa, Japan. Japanese IEP-PF
<i>Polyarthra</i> spp.	200	0.74	Lake Douh, Belg. Dumont et al. (1975)
<i>Testudinella patina</i>		0.05	Lake Suwa, Japan. Japanese IEP-PF
<i>Filinia longisetata</i>	100,200	0.42,0.48	Pond at Patan, Nepal. Dumont et al. (1975)
<i>F. longisetata</i>		0.15	Lake Suwa, Japan. Japanese IEP-PF
<i>Hexarthra fennica</i>	100,200	0.64,0.56	Aci Goi, Turkey. Dumont et al. (1975)
<i>H. mira</i>	100,200	0.85,1.04	Ag. Sidi Ali, Morocco. Dumont et al. (1975)
<i>H. mira</i>		0.20	Lake Suwa, Japan. Japanese IEP-PF
<i>Conochilus hippocrepis</i>		0.015	Lake Suwa
<i>Collotheca cornuta</i>		0.10	Lake Suwa

* Mean for $90 \pm \text{S.E.} : 6.62 \pm 0.07$

** Range for regression

*** 4 hours in 4% formaldehyde

**** 9 years in 4% formaldehyde

TABLE IX. Individual body wet weights from calculated volumes (mg) of freshwater Rotifera.

Species	Range of mean weight	Number of IBP sites
<i>Brachionus calyciflorus</i>	0.35-2.80	3
<i>B. angularis</i>	0.70	2
<i>Keratella quadrata</i>	0.07-0.64	6
<i>K. cochlearis</i>	0.05-0.62	9
<i>K. hiemalis</i>	0.05-0.30	3
<i>Kellicottia longispina</i>	0.10-0.25	6
<i>Notholca acuminata</i>	2.00	1
<i>N. squamula</i>	0.46	1
<i>N. grandis</i>	4.63	1
<i>N. caudata</i>	0.70	1
<i>N. intermedia</i>	0.21	1
<i>Trichocerca pusilla</i>	0.07	1
<i>T. rousseleti</i>	0.07	1
<i>T. porcellus</i>	0.10	1
<i>Asplanchna priodonta</i>	8.40-30.00	8
<i>A. girondi</i>	18.00	1
<i>Synchaeta pectina</i>	1.00	1
<i>S. lackowitziana</i>	1.00	1
<i>S. grandis</i>	1.00	1
<i>S. pachypoda</i>	7.00	1
<i>Synchaeta sp.</i>	0.50-2.00	3
<i>Polyarthra vulgaris</i>	0.27-0.92	6
<i>P. dolichoptera</i>	0.27-0.60	5
<i>P. major</i>	1.00	3
<i>P. remata</i>	0.50	2
<i>Filinia longispina</i>	0.30-0.45	3
<i>F. terminalis</i>	0.30-0.55	3
<i>Conochilus unicornis</i>	0.30-0.56	5
<i>C. hippocrepis</i>	0.60-0.80	2

rotifers as recorded in these data reports. Wet weights for the same species can vary in most cases by 2-4 times in different localities apart from *Keratella* spp. whose weight variation can be as high as 10 times. Methodological error superimposed upon biological variation may be the cause of such variability. One such cause lies in the choice of geometric shape, but whether this is so cannot be identified for the examples given in Table IX, since the geometric shapes employed were recorded in only two data reports. There seems to be a good case for establishing volume formulae for particular rotifer species which can be adopted by workers interested in comparability of data (see appendix by A. Ruttner-Kolisko). A second cause of variability may lie in the use of a specific

gravity of 1.0. This is no longer necessary as it is possible to obtain a non-osmotic solution, such as Ficoll, for producing a density gradient.

There are few records of dry weight/wet weight ratios for rotifers. A 10% ratio was obtained by Doohan (1973) for *Keratella quadrata*, *Polyarthra vulgaris*, *Synchaeta oblonga* and *Brachionus plicatilis* when she compared her measured dry weights with the wet weights for these species calculated from volumes given by Kosova (1961). This is illustrated in Fig. 4 together with the linear regression of dry weight on volume for *Asplanchna brightwelli* (Dumont et al. 1975), whose dry weight/wet weight ratio is only 3.9%.

There are very few records of protozoan weights; those recorded in Table VIII are dry weights (Japanese IBP/PF) and in general are one order of magnitude smaller than rotifers.

Body size of Crustacea

In the 24 IBP Data Reports containing information on crustacean sizes, the data varied from: (a) one mean weight for the whole species-population as it existed at one moment in time and including all the sizes present, (b) a series of mean weights for different instars or size classes to (c) a length/weight regression for a species, based upon all the stages of the life cycle but usually unaccompanied by the raw data, confidence limits or the range of sizes. The dry or wet weights were measured directly either on freshly killed or on preserved animals, usually formalin-fixed, or wet weights have been derived from the shapes in Chislenko's nomogram (Chislenko 1968) from which wet weight can be read for a given length. For comparability, it is important to know whether all these methods for obtaining weights provide interchangeable values of similar precision and accuracy. In addition, it is necessary to know whether the relationship between dry and wet weight remains the same throughout the life cycle and in different species. Although factors for converting wet or dry biomass into carbon or energy can be determined, their accuracy depends upon how reproducible the weights are.

Several workers have considered whether directly measured and volume-derived wet

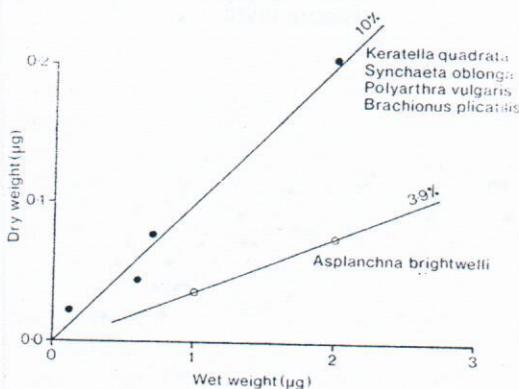


Fig. 4. The relationship between volume wet weight and dry weight in five species of rotifers. Modified from Dumont et al. 1975 and Doohan 1973.

weights give similar results. Karabin (1974) found that his calculated volumes for *Leptodora* provided wet weights which were similar to those obtained from Chislenko's nomogram although there was a tendency for the two length/weight regression lines to diverge for the larger sizes. However, directly measured wet weights of *Leptodora* (Cummins et al. 1969) fitted the Chislenko-derived data closely. Larsson compares an unpublished length/wet weight regression for *Bosmina longispina* from Øvre Heimdalsvatn with previously published length/volume regressions for *Bosmina longispina* (Shcherbakov 1952, Osmera 1966) and for *Bosmina* sp. (Pechen 1965). The volumes were converted to wet weights by assuming a specific gravity of 1.0. Three of the regressions gave similar results, but again with a tendency to diverge for the larger sizes; the Osmera regressions gave different values. A similar divergence for larger sizes was revealed when a length/wet weight regression for *Heterocope saliens* from Øvre Heimdalsvatn was compared with a length/volume regression for *Macrocylops albidus* (Klekowsky & Shushkina 1966), both of which included nauplii (Fig. 5).

The differential loss or retention of water makes it difficult to obtain reproducible measured wet weights. Individuals of different size may retain or lose water in different amounts depending on their surface area to volume ratios and the techniques used to remove 'excess water'. This may provide

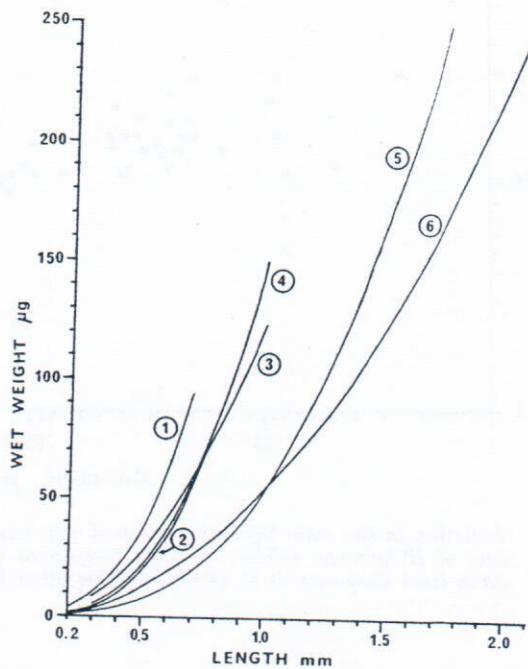


Fig. 5. Length/volume (V) and length/wet weight (W) regressions of planktonic crustacea according to various authors. Units: mm and μg . Volumes are converted to weight by assuming a specific weight of 1.

<i>Bosmina longirostris</i> (V)	
Osmera 1966	$W = (0.60 L + 0.035)^3 \cdot 10^3$
<i>Bosmina longirostris</i> (V)	
Sherbakow 1952	$W = (0.56 L - 0.01)^3 \cdot 10^3$
<i>Bosmina</i> (V)	
Pechen 1965	$W = 124 L^{2.181}$
<i>Bosmina longispina</i> (W)	
Ø. Heimdalsvatn	$W = 150 L^{2.809} \quad r = 0.897$
<i>Macrocylops albidus</i> (V)	
Klekowsky & Shushkina 1966	$W = 55 L^{2.73}$
<i>Heterocope saliens</i> (W)	
Ø. Heimdalsvatn	$W = 53 L^{2.106} \quad r = 0.945$

one explanation for the variability of dry weight/wet weight ratios reported in the literature, which appears to be confirmed by Fig. 6. Measured dry and wet weights for *Bosmina longispina* and *Heterocope saliens* (Larsson, unpublished) and for *Leptodora kindtii* (Cummins et al. 1969) provide the data for this figure, which demonstrates a trend of decreasing values for dry weight/wet weight ratios with increase in body size. The universally adopted 10% is applicable to only part of the total range of sizes in the life cycles. That this trend includes biological variation in these ratios is demon-

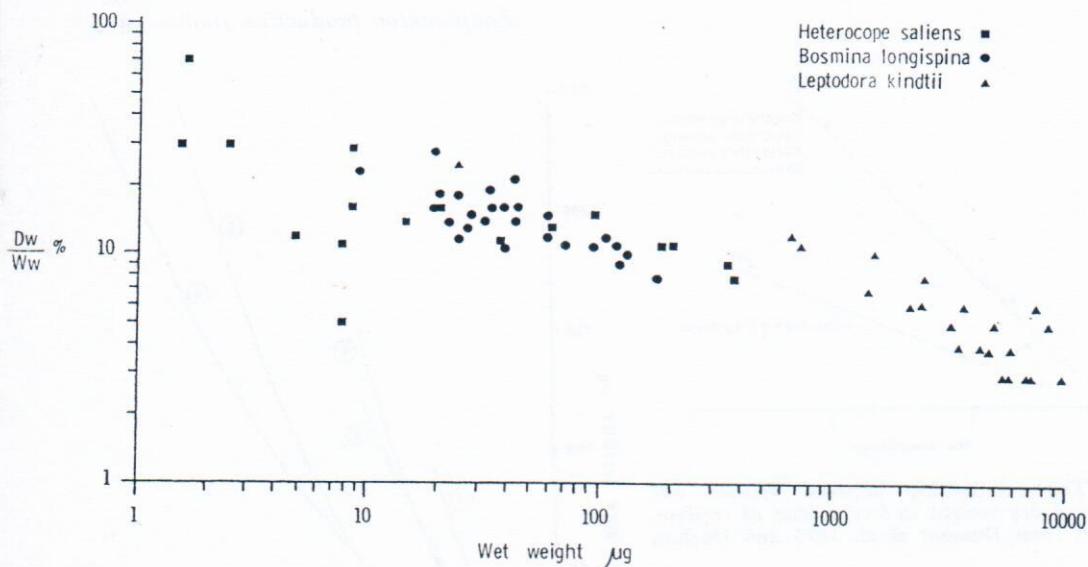


Fig. 6. Variation in the ratio between measured dry weight and measured wet weight for different sizes of *Heterocope saliens*, *Bosmina longispina* and *Leptodora kindtii*. (*Leptodora* data are taken from Cummins et al. (1969) and the other from Larsson (in manus.).)

strated in Fig. 7, where dry weight/volume ratios for *Cyclops scutifer* and *Heterocope saliens* show a similar downward trend with increase in size.

Several authors weighed preserved animals, most often formalin-fixed. Although Howmiller (1972) reports as much as a 50% loss of the initial wet weight and a 10% loss of dry weight of formaldehyde-fixed tubificids and chironomid larvae, formalin preservation does not appear to affect seriously the body weights of planktonic animals, especially if they were well-washed prior to weighing. Lebedeva & Kozlova (1969) measured fixed and fresh wet weights of a range of sizes of 15 species of Cladocera. The following regression ($Y = a + bX$, where Y is the fixed wet weight and X the fresh wet weight) is based upon their published data:

$$a \quad b \pm 95\% \text{ c.l.} \quad d.f. \quad F \quad P \\ 0.0233 \quad 1.0517 \pm 0.1912 \quad 1; 44 \quad 86 \quad 0.001$$

and demonstrates the similarity of the two weights. Other authors have compared fresh and fixed dry weights of planktonic crustaceans and found no detectable differences at the 5% level (Bottrell 1976).

Cladocera. — Table X presents a series of

length/dry weight regressions for freshwater Cladocera derived either from the literature or from original lengths and weights given to the Plankton Ecology Group by workers from IBP projects. Where raw data was available, a series of comparable regressions were obtained by employing the same units (mm, μg) and the same transformation. This enabled each regression to be tested for level of significance and for a comparison to be made of the confidence limits on the slopes and of the magnitude of the residual mean squares. For comparison, the values for the intercept of the published regressions have been transformed after conversion to the same units but for these there is neither any statistical information nor the range of sizes. All the regressions listed in Table X are significant and are available for species from three families of the Cladocera, although the Daphniidae have the most extensive coverage with three genera and nine species.

The Bosminidae are represented by two species from three localities. Both intercepts and slopes show a considerable range in values and the slopes have wide confidence limits (11–24% of the b -value), although the populations of *Bosmina longispina* from Øvre

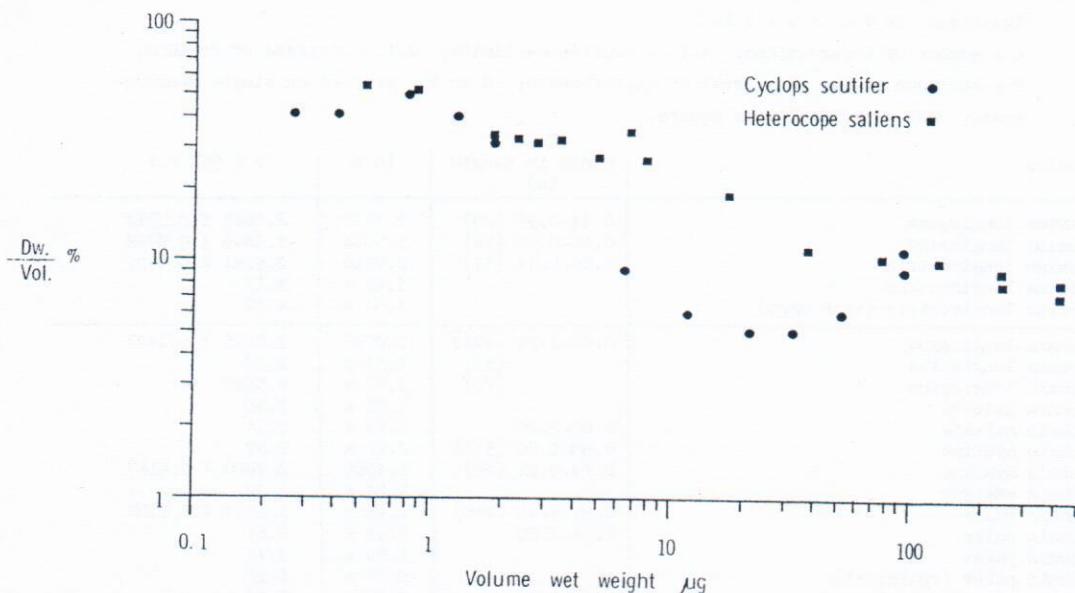


Fig. 7. Variation in the ratio between measured dry weight and calculated volume for different sizes of *Heterocope saliens* and *Cyclops scutifer*. The volumes are calculated from the regression given by Klickowski & Shushkina (1966). (Raw data from Larsson (in prep.)).

Heimdalsvatn and *Bosmina longirostris* from the River Thames are similar. The regression for bosminids based upon the pooled raw data provides a significant mean regression line with improved slope and confidence limits, and retains a low residual mean square; this is associated with the larger number of pooled observations and the wider range of sizes covered.

In contrast, the individual *Daphnia* regressions are more similar to each other than among the bosminids, both in intercept and slope. When plotted, these appear as a series of closely placed parallel lines. The other difference from the *Bosmina* regressions is the lower value of the intercept. This similarity among the *Daphnia* regressions is surprising as the number of observations per regression is variable, some being few in number, but all cover a wide range of sizes. Compared with *Bosmina*, all the *Daphnia* regressions show narrower confidence limits of the slope and higher variance ratios; this is also true of the pooled *Daphnia* regression. However, the level of unexplained variation (residual mean square) is much higher than for *Bosmina* in both the individual and pooled *Daphnia* regressions. The

nature of the original data probably influences this. Daphniids are large enough to weigh singly and their regressions are based upon individual values, which allows the total variance and residual mean square to be fully estimated. The smallness of bosminids means that their regressions are based upon mean lengths and weights of grouped individuals, resulting in spuriously low residual mean squares. Moreover, replication of grouped weights requires more work so the wider confidence limits of the regression coefficient probably arise from the lower number of observations. However, the level of significance of the regression is not affected.

The regressions for *Ceriodaphnia quadrangula* and *Diaphanosoma brachyurum* are similar to those for *Daphnia*, although the small range of sizes in *Ceriodaphnia* affects the slope and confidence limits; this will always be a problem in small species with large newly hatched young. Because body length is a difficult measure in *Holopedium gibberum*, the length of the abdomen has been adopted but this has resulted in an intercept value of a different order of magnitude. It appears to be a reliable measure judging from the low residual mean square.

TABLE X Linear regressions relating length (mm) with dry weight (μg) in freshwater Cladocera.Equation: $\ln W = \ln a + b \ln L$ n = number of observations; c.l. = confidence limits; d.f. = degrees of freedom;

F = variance ratio; P = level of significance; G or S = grouped or single measurements; RMS = residual mean square.

Species	Range in length (n)	$\ln a$	$b \pm 95\% \text{ c.l.}$
<i>Bosmina longispina</i>	0.44-0.95 (26)	2.7312	2.0665 ± 0.2312
<i>Bosmina longispina</i>	0.30-0.50 (34)	3.5274	3.5859 ± 0.8768
<i>Bosmina longirostris</i>	0.28-0.54 (17)	2.7116	2.5294 ± 0.5722
<i>Bosmina longirostris</i>		3.28 *	3.13
<i>Bosmina longirostris</i> (with eggs)		4.68 *	4.27
<i>Daphnia longispina</i>	0.60-2.35 (404)	1.0727	2.8915 ± 0.1421
<i>Daphnia longispina</i>	(37)	1.34 *	2.57
<i>Daphnia longispina</i>	(75)	1.37 *	2.5567
<i>Daphnia galeata</i>		1.51 *	2.56
<i>Daphnia galeata</i>	0.60-2.20	2.64 *	2.54
<i>Daphnia hyalina</i>	0.60-2.20 (372)	2.46 *	2.52
<i>Daphnia hyalina</i>	0.78-2.21 (22)	1.4369	2.7680 ± 0.4167
<i>Daphnia ambigua</i>		1.54 *	2.29
<i>Daphnia pulex</i>	0.95-3.40 (245)	1.4663	3.1932 ± 0.1798
<i>Daphnia pulex</i>	0.55-1.60	2.48 *	2.63
<i>Daphnia pulex</i>		1.59 *	2.77
<i>Daphnia pulex</i> (ephippial)		-0.71 *	3.13
<i>Daphnia schoelleri</i>	1.00-2.50	2.30 *	3.10
<i>Daphnia magna</i>	0.82-4.00 (245)	1.6729	2.6880 ± 0.1429
<i>Daphnia magna</i>	0.84-4.83 (516)	1.8268	2.7854 ± 0.0627
<i>Daphnia magna</i>		2.20 *	2.63
<i>Daphnia magna</i>	1.40-3.60	2.51 *	1.80
<i>Daphnia magna</i>		2.36 *	2.25
<i>Daphnia magna</i> (ephippial)		2.12 *	2.61
<i>Ceriodaphnia quadrangula</i>	0.30-0.71 (19)	2.5623	3.3380 ± 0.6819
<i>Diaphanosoma brachyurum</i>	0.44-1.44 (106)	1.6242	3.0468 ± 0.3025
<i>Holopedium gibberum</i>	0.08-0.43 (8)	5.3976	2.0555 ± 0.3754
<u>Pooled data:</u>			
<i>Bosmina</i> spp	0.28-0.95 (77)	3.0896	3.0395 ± 0.2123
<i>Daphnia</i> spp		1.60 *	2.84
<i>Daphnia</i> spp		2.45 *	2.67
<i>Daphnia</i> spp (with eggs, embs, ov.)	0.60-4.83 (1128)	1.7769	2.7166 ± 0.0634
<i>Daphnia</i> spp (without eggs, embs, ov.)	0.60-4.00 (1303)	1.4681	2.8292 ± 0.0723
<i>Daphniidae</i> (without eggs, embs, ov.)	0.30-4.00 (1322)	1.5072	2.7610 ± 0.0683
<i>Daphniidae</i> (without eggs, embs, ov.) + <i>Sididae</i>	0.28-4.00 (1438)	1.5163	2.7515 ± 0.0620
<i>Cladocera</i>	0.28-4.83 (1756)	1.7512	2.6530 ± 0.0593

NOTES: The following persons have provided or calculated regressions (marked *) or raw data from which regressions have been calculated by the authors; published regressions are also marked with an *.

L: P. Larsson, H: A. Herzig, W: R. White, M: I. Munro, K: H. Kurasawa, A: T. E. Andrew,
B: H. H. Bottrell, D: A. Duncan.

There were only a few observations which influenced the confidence limit of the slope.

All the cladoceran raw data, apart from *Holopedium gibberum*, was used to calculate a cladoceran regression which is given in

Table X. Although it has satisfactorily narrow confidence limits of the slope, the residual mean square is larger than expected. The cause of this is demonstrated in Fig. 8, where the *Bosmina* and *Daphnia* pooled re-

d.f.	F	P	RMS	G or S	Locality (Author)
1;24	322	0.001	0.0172	G	Øvre Heimdalsvatn (L)
1;32	70	0.001	0.0936	G	Neusiedlersee (H)
1;15	88	0.001	0.0501	G	River Thames (B) Lake Donk (Dumont et al., 1975) Lake Donk (Dumont et al., 1975)
1;402	1590	0.001	0.1550	S	Lake Shirakomanoike (K) Rymeads Sewage lagoons (W) Bough Beech Reservoir (M) Lake Donk (Dumont et al., 1975) (Burns, 1969)
1;73	423	0.001			Queen Mary Reservoir (A) River Thames (B)
1;20	191	0.001	0.0809	S	Lake Donk (Dumont et al., 1975) Queen Elizabeth II Reservoir (D) (Burns, 1969)
1;243	1212	0.001	0.1629	S	Lake Donk (Dumont et al., 1975) Lake Donk (Dumont et al., 1975) (Burns, 1969)
1;243 1;514	1359 6902	0.001 0.001	0.1860 0.0913	S S	Queen Mary Reservoir (D) Queen Elizabeth II Reservoir (D) (Burns, 1969) River Sambre (Dumont et al., 1975) Lake Donk (Dumont et al., 1975) Lake Donk (Dumont et al., 1975)
1;17	107	0.001	0.1463	G	Neusiedlersee (H)
1;104	1488	0.001	0.1370	G	Neusiedlersee (H)
1;6	179	0.001	0.0577	G	Øvre Heimdalsvatn (L)
1;75	787	0.001	0.0867		2 spp (1) - (3)
1;1126 1;1301	7045 5856	0.001 0.001	0.2098 0.2658	S	4 spp (5),(8),(10),(13) 4 spp Burns (1969) 3 spp (9),(11),(12) + <u>D.hyalina</u> 4 spp (4),(7),(9),(11),(12) + <u>D.hyalina</u>
1;1320 1;1426	6279 7569	0.001 0.001	0.2705 0.2613		5 spp (4),(7),(9),(11),(12),(14) + <u>D.hyalina</u> 6 spp (4),(7),(9),(11),(12),(14),(15) + <u>D.hyalina</u>
1;1754	7182	0.001	0.4542		8 spp (1) - (4), (6),(7),(9),(11),(12),(14),(15)

gression lines have been plotted for the range of sizes involved. The bosminid regression has a higher elevation than the *Daphnia* one, which implies that all sizes are heavier per unit length than the daphniids; this may be associated with their stouter carapaces. The larger number of daphniid observations greatly influences the total cladoceran regression, which therefore predicts weights that are too low for *Bosmina*. A total cladoceran regression is of less utility than the separate pooled *Bosmina* and *Daphnia* regressions for pre-

dicting weight from length. However, judging from the regressions obtained by pooling *Ceriodaphnia* with *Daphnia* data (the Daphnidae) or pooling daphnid with *Diaphanosoma* data (the Daphnidae and Sididae), some other cladoceran genera and families do have similar length/dry weight regressions with narrow confidence limits of the slope and low residual mean squares. The removal from the pooled data of *Daphnia* individuals with ovaries, eggs or embryos affects neither the confidence levels nor the residual mean

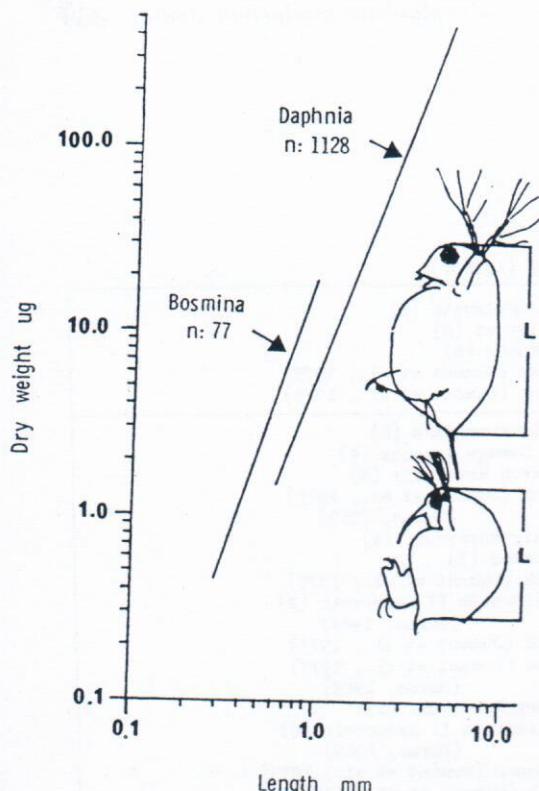


Fig. 8. Regression lines for pooled data on length/weight relationships in *Daphnia* and *Bosmina*. The equations used are taken from Table VIII.

square, seems to make no significant difference to the value of the intercept but does produce a significant difference in the slope.

Some other factor than length is influencing weight in the populations of *Daphnia longispina* from Lake Shirakomanoike in Japan (Kurasawa, raw data). Table XI shows that the mean size per individual decreased from May to July due to the loss of larger sizes for some unknown reason. The length/dry weight regressions based on monthly samples are all significant, possess a common slope, but have different elevations. There occurred a depression of the regression elevation from May to July as larger sizes were lost and the mean size decreased, demonstrating a monthly change in the weight per unit length. The elevation for the September sample returned to its July level and coincided with an increase in mean size.

Copepoda. — In Table XII length/dry weight

regressions are given for 11 copepod species based upon raw data from some IBP projects: these were manipulated in a similar way to the cladoceran regressions.

All but one of these regressions are significant. Provided that the regression covers the whole life cycle, the angle of the slope, although somewhat less steep, does not appear to be different from that of the Cladocera. The same can be said of the confidence limits of the slope (varying between 4–21% of the b-value) and the magnitude of the residual mean square.

Compared with the other copepod regressions covering the whole life cycle, that for *Cyclops scutifer* shows both wider confidence limits about a flatter slope and a higher residual mean square. When separate regressions for nauplii, and copepodites plus adults were plotted (Fig. 9), the cause of the greater unexplained variation became apparent. There was a discontinuity in total length between the largest naupliar and smallest copepodite stages, which corresponded to the length of the furcal rami (about 0.1 mm) present in the copepodite but not in the nauplius. The discontinuity arose because there was no corresponding increase in weight to the addition in length. Under these circumstances, the separate regressions are better as they fit the original data more closely. In the case of *Heterocope saliens*, the regression covering the whole life cycle provided a better fit than the separate naupliar and copepodite plus adult regressions because, in this species, the furcal rami are shorter than in *Cyclops scutifer*, resulting in a less pronounced discontinuity. The wider range of sizes available throughout the life cycle improves the estimation of the regression coefficient and prevents the calculation of aberrant b-values in regressions covering the larger sizes only.

Total length was measured in *Cyclops scutifer* and *Heterocope saliens*. A better measure of length may eliminate the problem of discontinuity in the total length/dry weight regression line, for example, by excluding the furcal rami (Burgis 1974) or by including only the free thoracic segments (Herzig 1974). In Fig. 9, which gives plots of all the available regressions, much of the variation in slope and intercept might be due to the different measurements of length adopted.

TABLE XI

Linear regressions relating length (mm) to dry weight (μg) in Daphnia longispina from Lake Shirakomoike, Japan (from H.Kurasawa). Equation: $\ln W = \ln a + b \ln L$.

\bar{L} = mean length; \bar{W} = mean weight; n = number of observations; c.l. = confidence limits; d.f. = degrees of freedom; F = variance ratio; P = level of significance; RMS = residual mean square.

Date	\bar{L}	\bar{W}	n	$\ln a$	$b \pm 95\% \text{ c.l.}$	d.f.	F	P	RMS
30.5.74	1.47	12.97	98	1.5499	2.6136 ± 0.2342	1 ; 96	503	0.001	0.0983
30.6.74	1.14	4.26	110	1.0979	2.6040 ± 0.2782	1 ; 108	347	0.001	0.1380
30.7.74	1.22	3.81	99	0.8165	2.6780 ± 0.2898	1 ; 97	338	0.001	0.0725
3.9.74	1.28	5.61	97	1.0792	2.6420 ± 0.1825	1 ; 95	829	0.001	0.0702
All dates pooled	1.27	5.80	404	1.0727	2.8915 ± 0.1421	1 ; 402	1590	0.001	0.1550

DEVELOPMENT TIMES

The static picture given by standing crop data is of limited application to the interpretation of dynamic systems. Development times when combined in various ways with data on density and individual weight provide the time element necessary for the calculation of instantaneous birth, death and growth rates, and the production of continuously reproducing species (see Edmondson 1960, Hillbricht-Ilkowska & Patalas 1967, Paloheimo 1974).

There is a fundamental difference between the duration of embryonic and post-embryonic development in that in many poikilotherms the duration of egg development is a significant function of temperature, whereas the duration of post-embryonic development is a function of both temperature and food. However, the effect of a change in temperature is the same in both cases.

Egg development

Variation in the duration of egg development both within and between species is attributable to two major sources; methodological errors involved in measuring the egg development times, and natural variation. The potential sources of methodological error are:

(1) the type of animal used, that is, whether measurements are made on animals main-

tained wholly in the laboratory (e.g. Pourriot & Deluzarches 1971), or on animals brought in from the field and maintained in the laboratory at a temperature close to that of the habitat from which they were collected (e.g. Duncan et al. 1970, Munro 1974, Duncan 1975b). In the latter case, ovaries will have been grown on natural food at field concentrations which may affect egg size;

(2) whether egg development time is calculated by observing a number of specimens at frequent intervals and regressing the number of females remaining with eggs against time (e.g. Burgis 1970), or by observing the time between laying and hatching of individual specimens (e.g. Bottrell 1975b);

(3) the time interval between successive observations. Two sources of natural variation in egg development times have been demonstrated. These are: temperature and egg size; with variations in temperature often explaining in excess of 80–90% of variations in the duration of egg development.

Data on the mean duration of egg development time in relation to temperature has been collated from a total of 91 data sets (35 copepods, 34 cladocerans and 24 rotifers) which cover 59 species (21 copepods, 23 cladocerans and 15 rotifers). For purposes of presentation the data has been split into five groups: Daphnidae, other Cladocera, Cyclopoida, Calanoida and Rotifera (Figs. 10–14). The majority of the data is for temperate

TABLE XIII Linear regression relating length (mm) with dry weight (μg) in freshwater Copepoda.

$$\text{Equation: } \ln W = \ln a + b \ln L$$

W = weight; L = length; 1) only free thoracal segments measured; 2) length do not include furcal rami; the rest are total lengths including rami, but not terminal setae; n = number of observations; c.l. = confidence limits; d.f. = degrees of freedom; F = variance ratio; P = level of significance; RMS = residual mean square.

Species	Instars	Range of L (n)	$\ln a$	$b \pm 95\% \text{ c.l.}$	d.f.
Heterocope saliens	N1-N6	0.18-0.79 (9)	2.0365	1.8911 ± 0.3790	1;7
	CI-ad	0.66-2.08 (8)	1.8977	2.0374 ± 0.2276	1;6
	N1-ad	0.18-2.08 (17)	1.8551	1.9756 ± 0.0890	1;15
Diaptomus gracilis	N-ad	0.30-1.85 (23)	1.2431	2.2634 ± 0.3212	1;21
1) Arctodiaptomus spinosus	C ad ♂ ad ♀ C-ad	0.32-0.60 (48) 0.65-1.02 (86) 0.76-1.16 (107) 0.32-1.16 (241)	2.8519 2.3409 2.2614 2.3392	3.6520 ± 0.9771 2.4409 ± 0.4206 3.5724 ± 0.4267 2.9835 ± 0.1067	1;46 1;84 1;105 1;239
2) Thermocyclops hyalinus	C-ad	0.31-0.68 (25)	0.6772	0.8928 ± 0.6408	1;23
2) Mesocyclops leuckarti	C-ad	0.33-1.14 (23)	1.2700	2.2570 ± 1.5074	1;21
2) Cyclops vernalis	CV-ad	1.22-1.73 (21)	2.4511	0.7825 ± 0.4444	1;9
2) Cyclops viridis	ad (3 with eggs)	1.60-2.45 (29)	2.7412	1.6785 ± 1.0910	1;27
2) Cyclops vicinus	N-CV N-♀ with eggs ♀ with eggs ad ♀	0.17-1.60 (27) 0.17-2.18 (111) 1.25-2.18 (84) 1.12-2.18 (120)	1.4497 2.0577 2.4342 2.0186	2.1160 ± 0.1189 2.5530 ± 0.0923 1.9694 ± 0.4705 1.9948 ± 0.4884	1;25 1;109 1;82 1;118
Cyclops scutifer	N1-N6 CI-ad N1-ad	0.14-0.29 (6) 0.45-1.20 (7) 0.14-1.20 (13)	2.5442 1.2286 1.0866	2.3696 ± 0.7492 2.6398 ± 0.8321 1.5493 ± 0.3324	1;4 1;5 1;11
Cyclops strenuus	N-ad	0.24-1.72 (20)	1.5386	2.3418 ± 0.2575	1;18
Cyclops abyssorum	CII-ad	0.66-1.70 (52)	2.2128	2.2947 ± 0.2575	1;50
POOLED DATA: Copepoda (÷ ♀ with eggs)	N1-ad	0.14-2.45 (535)	1.9526	2.3990 ± 0.0854	1;535

The following persons have provided raw data: B: H.H. Bottrell; Bu: M.J. Burgis; H: A. Herzig;
L: P. Larsson; W: A. Walker.

water bodies with a few studies in polar and tropical water bodies extending the temperature range. The data sources are given below each graph. Some previously unpublished data is presented in Table XIII. Only one set of unpublished data for resting eggs was available to the authors.

In each group a decrease in temperature results in an increase in both the duration of egg development and the absolute variation between species. The increasing variation below 5°C is based on few observations and thus is difficult to interpret, but it is probably due to technical difficulties and/or increased variation in egg size at low temperatures. Increases in egg development time

at high temperature have been reported for *Arctodiaptomus salinus* (Elster & Vollenweider 1961) and *Thermocyclops hyalinus* (Burgis 1970). This is probably a universal feature which would be observed more frequently if experimental temperature in excess of 30°C were used more frequently.

The increasing variation with decreasing temperatures creates problems for the mathematical description of the relationship between the duration of egg development and temperature. Bottrell (1975a) has shown that with such a pattern of variation a reciprocal function is unsuitable for describing the relationship and that a curvilinear logarithmic function is more appropriate. It was also

F	P	RMS	Water body (author)
132	0.001	0.0238	Ø. Heimdalsvatn (L)
460	0.001	0.0112	
1972	0.001	0.0190	
213	0.001	0.1422	River Thames (B)
57	0.001	0.1699	Neusiedlersee (H)
135	0.001	0.0284	
278	0.001	0.0497	
2778	0.001	0.0729	
44	0.001	0.1131	Lake George (Bu)
134	0.001	0.1031	
0.66	0.50	0.2123	London Reservoir (Bu)
11	0.005	0.0837	
1336	0.001	0.0578	
2938	0.001	0.0471	
67	0.001	0.2400	
64	0.001	0.2471	
76	0.001	0.0257	Ø. Heimdalsvatn (L)
67	0.001	0.0782	
105	0.001	0.1652	
362	0.001	0.0757	River Thames (B)
305	0.001	0.0806	Loch Leven (W)
3030	0.001	0.2570	

shown that Krogh's curve and the vant' Hoff-Arrhenius functions were not suitable for describing the relationship.

For the present data, a logarithmic transformation was applied to both the dependent and independent variable, and linear and curvilinear regressions fitted to each group and several pooled groups. An analysis of variance shows that a significant degree of curvilinearity exists for each group and for the pooled groups (Table XIV). The curvilinear regressions relating duration of egg development to temperature (Table XV) were used to compute the predicted egg development times over the temperature range for which data were available. A comparison of the back-transformed predicted values

(Fig. 15) shows a marked similarity in the egg development times of the Cladocera and Copepoda between 5°C and 30°C. A detailed comparison of the regression was not realistic since the data were restricted to mean values. However, fitting a single line to the data for the crustacean groups as against individual lines for each group did not greatly increase the residual variation.

At a more detailed level it has been shown that there are differences both within and between species. Munro & White (1975) showed that there were significant differences in the duration of egg development of *Daphnia longispina* collected from two habitats but held under identical laboratory conditions. Bottrell (1975a) showed by comparison of regressions that the relationship between duration of egg development and temperature for nine species kept under similar laboratory conditions could be described properly only by individual regression lines, that is, there were significant differences between species. These results suggest that the differences are unlikely to be due to methodological errors, since the same procedure was used within each study. Munro & White (1975) suggest that these small scale differences in the duration of egg development may be due to differences in egg size. Bottrell (1975a) has since discovered that some of the differences between the nine species from the River Thames can be explained by differences in egg size; the larger eggs taking longer to develop than smaller eggs at a given temperature. Variations between species in egg size are probably related to the evolution of different reproductive strategies, whereas differences within the species are probably caused by differences in temperature, food and genotype, which affect both the metabolism and the strategy of egg production.

In the absence of detailed information on the development times for a species in a particular water body, is it valid to predict egg development times using a generalized regression line derived from values taken from the literature and pooled? At the detailed level using individual values rather than means it can be demonstrated that there are significant statistical differences both for the same species and between species. This means that a generalized regression will be

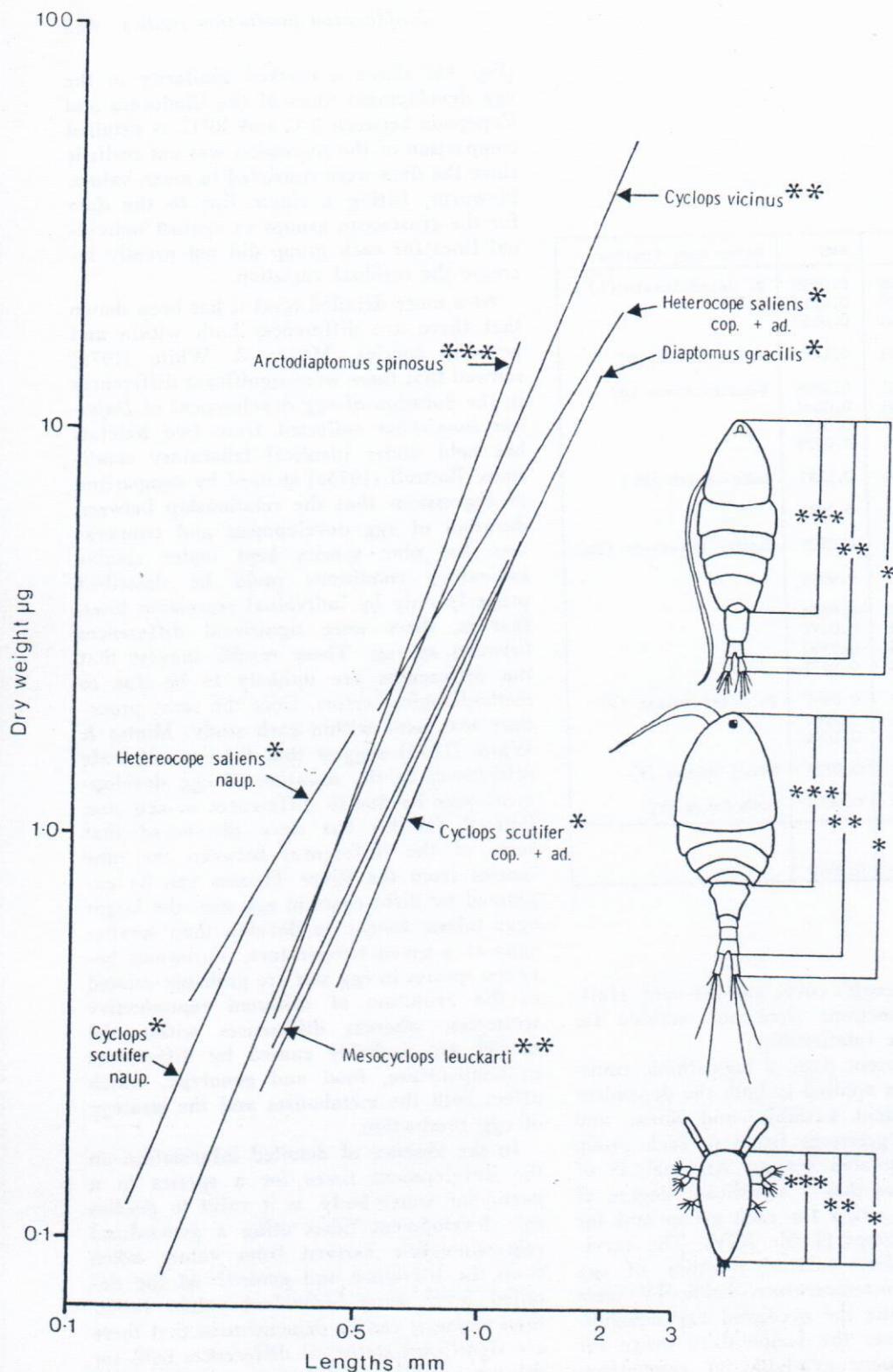


Fig. 9. Regression lines for individual species of Copepoda. The equations used are taken from Table X.

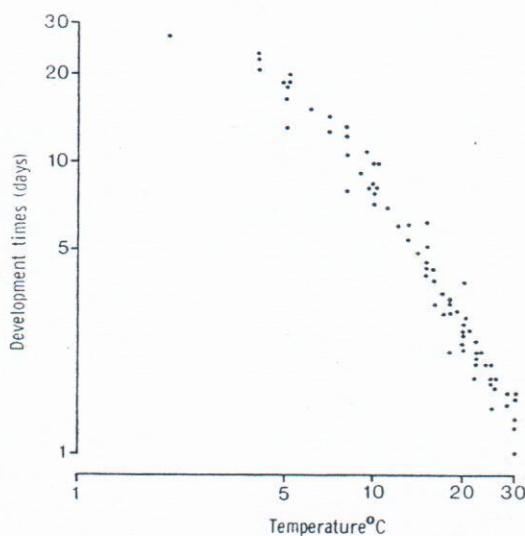


Fig. 10. The duration of egg development at various temperatures for 12 species of Daphniidae.

Sources of data: *Daphnia longispina* - Gras & St.-Jean 1969, Elster & Schwoerbel 1970, Weglenska 1971, Munro & White 1975; *Daphnia galeata mendotae* - Hall 1964; *Daphnia hyalina* - Korinek 1970, George & Edwards 1974, Duncan this paper; *Daphnia pulex* - Esslová 1959, Duncan this paper; *Daphnia magna* - Duncan this paper; *Daphnia barbata* - Gras & St.-Jean 1969; *Daphnia lumholtzi* - Gras & St.-Jean 1969; *Daphnia oucellata* - Weglenska 1971; *Ceriodaphnia cornuta* - Gras & St.-Jean 1969; *Ceriodaphnia affinis* - Gras & St.-Jean 1969; *Simocephalus vetulus* - Bottrell 1975b; *Simocephalus serrulatus* - Ang & Fernando 1973.

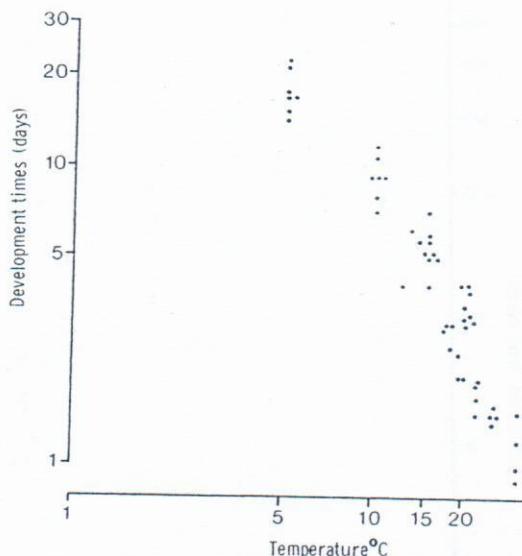


Fig. 11. The duration of egg development at various temperatures for 11 other Cladocera.

Sources of data: *Sida crystallina* - Bottrell 1975b; *Diaphanosoma excisum* - Elster & Vollenweider 1961, Gras & St.-Jean 1969; *Diaphanosoma brachyurum* - Weglenska 1971, Herzog raw data; *Bosmina longirostris* - Gras & St.-Jean 1969; *Moina micrura* - Gras & St.-Jean 1969; *Eury cercus lamellatus* - Smirnov 1962, Kryuchkova 1969, Petrovich & Nguen Chong 1971, Bottrell 1975b; *Alona affinis* - Bottrell 1975b; *Acroporus harpae* - Bottrell 1975b; *Graptoleberis testudinaria* - Bottrell 1975b; *Chydorus sphaericus* - Weglenska 1971, Bottrell 1975b; *Pleurexus uncinatus* - Bottrell 1975b.

TABLE XIII Curvilinear regressions relating duration of egg development (days) to temperature ($^{\circ}\text{C}$). Equation: $\ln D = \ln a + \ln T + c (\ln T)^2$.

n = number of observations; cl = confidence limit; df = degree of freedom; F = variance ratio; Level of significance: 0.001.

Group	Range (n)	$\ln a$	$b \pm 95\% cl$	$c \pm 95\% cl$	df	F
Rotifera	0.5 - 25 (88)	2.7547	- 0.2484 \pm 0.3341	- 0.2408 \pm 0.0861	2; 78	187
Daphniidae	2 - 30 (80)	3.3956	0.2193 \pm 0.3363	- 0.3414 \pm 0.0706	2; 77	1624
Other Cladocera	5 - 30 (55)	2.3279	1.2472 \pm 1.1046	- 0.5647 \pm 0.2237	2; 52	329
All Cladocera	2 - 30 (135)	3.1457	0.4797 \pm 0.3935	- 0.4003 \pm 0.0817	2; 132	1420
Calanoida	1 - 31 (121)	3.9650	- 0.4049 \pm 0.2738	- 0.1909 \pm 0.0625	2; 118	841
Cyclopoida	2 - 35 (74)	4.1301	- 0.4141 \pm 0.6861	- 0.2159 \pm 0.1424	2; 71	368
All Copepoda	1 - 35 (195)	3.9673	- 0.3479 \pm 0.2700	- 0.2145 \pm 0.0593	2; 192	1152
All Crustacea	1 - 35 (330)	3.7946	- 0.1487 \pm 0.2191	- 0.2627 \pm 0.0470	2; 327	2336

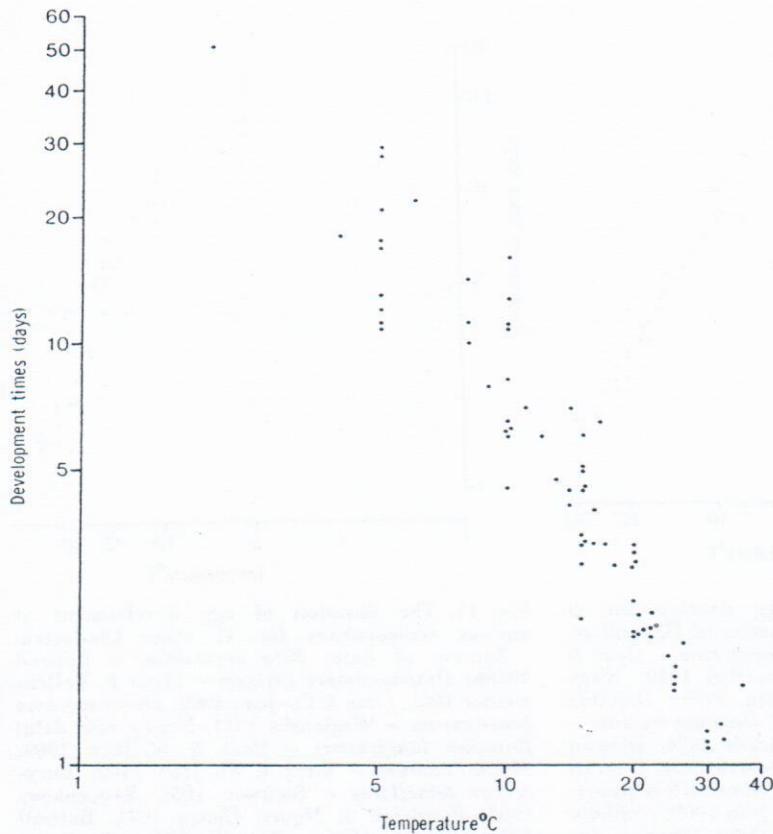


Fig. 12. The duration of egg development at various temperatures for 10 species of Cyclopoida.

Sources of data: *Thermocyclops hyalinus* – Burgis 1970; *Thermocyclops incisus* – Gras & St.-Jean 1969; *Thermocyclops neglectus* – Gras & St.-Jean 1969; *Mesocyclops leuckarti* – Einsle 1964, Taube & Nauwerck 1967, Gras & St.-Jean 1969, Vijverberg in Tjeukemeer IBP study; *Mesocyclops edax* – Carter 1974; *Acanthocyclops robustus* – Vijverberg in Tjeukemeer IBP study; *Cyclops vicinus* – Einsle 1964, Spindler 1971, Munro 1974; *Cyclops scutifer* – Taube & Nauwerck 1967; *Cyclops abyssorum* – Einsle 1964, Smyly 1973, Vijverberg in Tjeukemeer IBP study; *Eucyclops agilis* – Bottrell 1975b.

statistically invalid. However, at a general level using mean values (as these were the form of the published data) the similarity between crustacean groups over a wide range of temperature is striking. Although the level of unexplained variation for the generalized regression ($RMS<0.08$) is higher than that for individual regressions for each species ($RMS<0.02$, see Bottrell 1975a, Table 6), this is largely due to the use of mean values rather than the individual values. In the one case where the residual mean squares for the individual regression lines for nine species and the residual mean square for a common

line for the same nine species were available, it was found that the residual mean squares were very similar, but that there were significant differences between individual regression lines (Bottrell 1975a). Such a situation arises because the duration of egg development is a variable which is measured easily and with high precision; thus it is easy to obtain a significant difference between very similar values. Although the answer to the initial question is that in a strict statistical sense it is invalid to use the generalized regression, it is probably more sensible to ask the question: Is it sufficiently

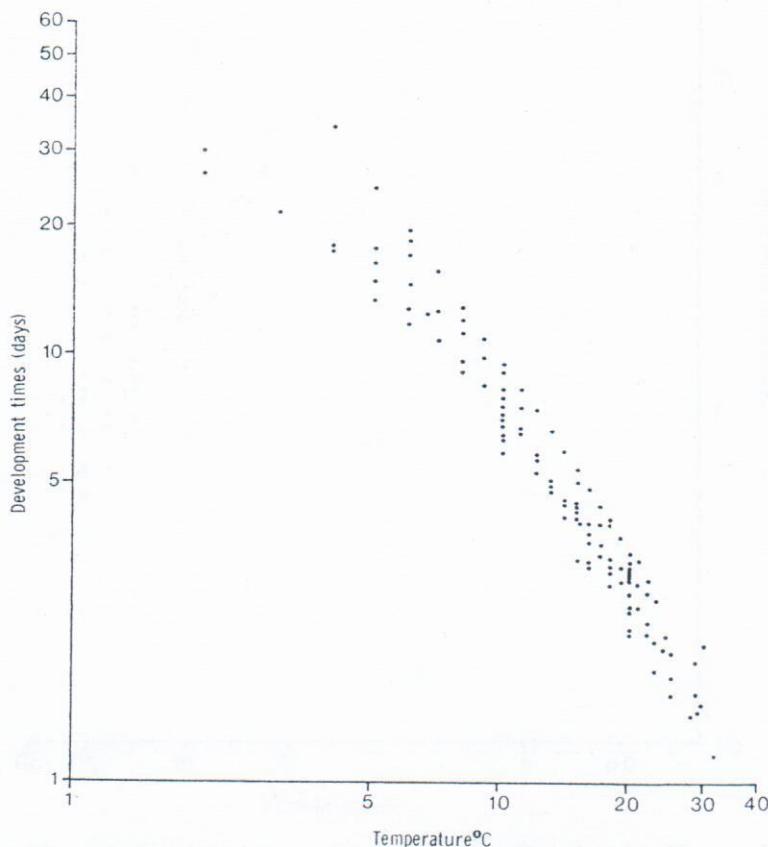


Fig. 13. The duration of egg development at various temperatures for 11 species of Calanoida.

Sources of data: *Diaptomus gracilis* — Elster 1954, Eckstein 1964, Munro 1974, Bottrell this paper; *Diaptomus graciloides* — Nauwerck 1963, Weglenska 1971; *Diaptomus minutus* — Schindler 1972; *Diaptomus orogensis* — Schindler 1972; *Diaptomus pallidus* — Geiling & Campbell 1972; *Diaptomus reighardi* — Carter 1974; *Acanthodiaptomus denticornis* — Eichhorn 1957; *Arctodiaptomus spinosus* — Herzig raw data; *Arctodiaptomus salinus* — Elster & Vollenweider 1961; *Mixodiaptomus lacinatus* — Eichhorn 1957; *Tropodiaptomus incognitus* — Gras 1970.

accurate to use a generalized regression line? The similarity and low residual mean squares of the generalized regression suggest that in the absence of detailed information on a particular species, a reasonably accurate prediction of egg development time can be obtained using a generalized regression within the temperature range for which it was calculated.

Post-embryonic development

The same sources of variation as apply to post-embryonic development apply also to embryonic development, but with the major addition of food as an important regulation

factor. Investigations of post-embryonic development times have considered either the effect of various food concentrations at one temperature (e.g. Weglenska 1971), or the effect of various constant temperatures under excess food conditions (e.g. Bottrell 1975b). The effects of food and temperature do not appear to have been studied simultaneously.

The data available on post-embryonic development times are both less numerous and more variable than the data on egg development times. The increased variation is probably attributed to food effects since most studies use an undefined food level which is usually assumed to be non-limiting, even

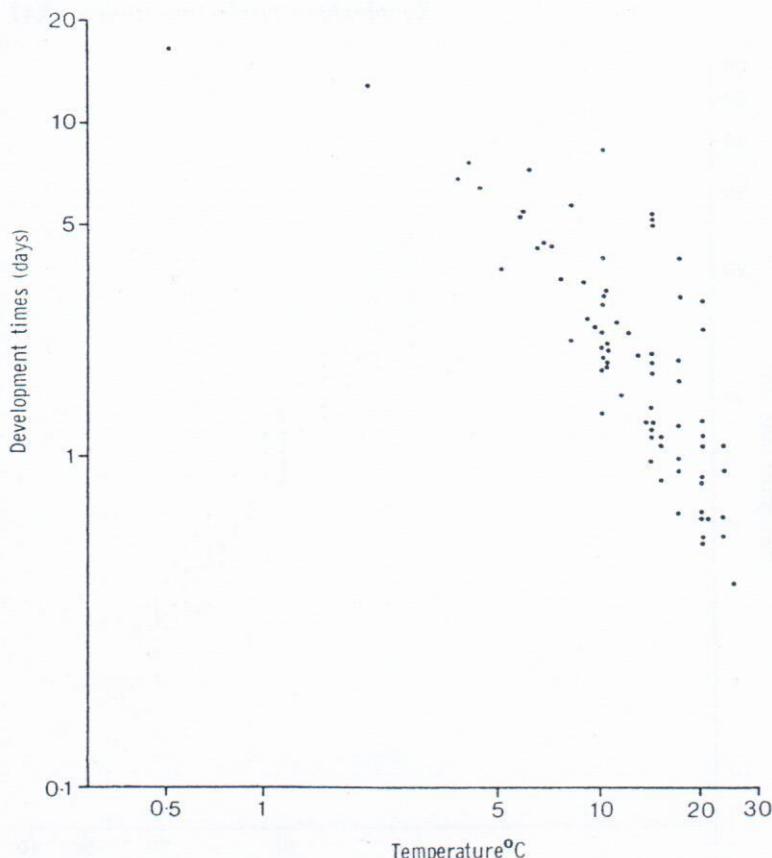


Fig. 14. The duration of egg development at various temperatures for 15 species of Rotifera.

Sources of data: *Brachionus calyciflorus* — Halbach 1970, Pourriot & Deluzarches 1971, Bottrell this paper; *Keratella cochlearis* — Edmondson 1960, Rigler et al. 1974; *Keratella quadrata* — Amréen 1964, Pourriot & Deluzarches 1971, Doohan 1973; *Keratella valga* — Pourriot & Deluzarches 1971; *Kellicottia longispina* — Edmondson 1960; *Notholca acuminata* — Pourriot & Deluzarches 1971; *Euchlanis dilatata* — Pourriot & Deluzarches 1971, Bottrell this paper; *Ploesoma hudsoni* — Edmondson 1960; *Ploesoma truncatum* — Edmondson 1960; *Epiphantes brachionus* — Pourriot & Deluzarches 1971; *Polyarthra dolichoptera* — Amréen 1964, Pourriot & Deluzarches 1971; *Synchaeta pectinata* — Pourriot & Deluzarches 1971; *Hexartra fennica* — Edmondson 1960; *Notommata collaris* — Pourriot & Deluzarches 1971; *Notommata capensis* — Pourriot & Deluzarches 1971.

though high food concentrations do not ensure adequate food quality.

It has been shown that under non-limiting food conditions the duration of post-embryonic development is highly dependent on temperature (Hall 1964, Korínek 1970, Bottrell 1975c); an increase in temperature causing a decrease in development time. The effects of various concentrations of food on post-embryonic development were investigated by Weglenska (1971). She found that the duration of post-

embryonic development increased by as much as three times with a decrease in food concentration; that above certain levels of food concentration there was little increase in development time, and that at very low food concentrations development may stop.

It is not clear from existing studies how often food-limiting conditions are encountered in nature, or what the alternative strategies in various food concentrations are. For instance: can Cladocera vary the number of

TABLE XIV

Analysis of variance - test for curvilinearity of the relationship $\ln D = \ln a + b \ln T + c (\ln T)^2$. All groups show a significant decrease in residual variation due to adding the quadratic term: $c (\ln T)^2$ to the linear equation.

df = degrees of freedom; MS = mean square; F = variance ratio; P = level of significance.

Group	Source of Variation	df	MS	F	P
Rotifera	Decrease due to quadratic	1	2.9025	14.83	0.001
	Residual due to quadratic	85	0.1957		
Daphniidae	Decrease due to quadratic	1	1.6548	92.45	0.001
	Residual due to quadratic	77	0.0179		
Other Cladocera	Decrease due to quadratic	1	1.3617	25.74	0.001
	Residual due to quadratic	52	0.0529		
All Cladocera	Decrease due to quadratic	1	3.0295	92.17	0.001
	Residual due to quadratic	132	0.0329		
Calanoida	Decrease due to quadratic	1	1.5509	35.88	0.001
	Residual due to quadratic	118	0.0432		
Cyclopoida	Decrease due to quadratic	1	0.6942	9.09	0.005
	Residual due to quadratic	71	0.0763		
All Copepoda	Decrease due to quadratic	1	3.2479	38.94	0.001
	Residual due to quadratic	198	0.0834		
All Crustacea	Decrease due to quadratic	1	6.1926	96.68	0.001
	Residual due to quadratic	333	0.0641		

juvenile instars to suit prevailing food conditions, or, do they have a fixed number of instars whose duration may vary with food concentration and temperature? It would be interesting to study the effects of food and temperature on the cyclopoid populations which have been shown to have prolonged cycles of more than one year (e.g. Elgmork 1965, Nauwerck 1967).

Some indication of post-embryonic development times may be determined from instar analysis of field data which would incorporate the influences of both food and temperature. There is, however, always a dispersion in time of development, even in fairly synchronized populations, and the precision of development times from field studies is usually less than from laboratory studies, although very frequent sampling increases the precision.

SUMMARY AND RECOMMENDATIONS

The problems associated with the measurement of standing crop, individual weights

and development times are reviewed within the context of attaining absolute comparisons between water bodies. The International Biological Programme has provided the possibility of making comparisons between water bodies, but comparisons are difficult because many different techniques and strategies have been used to measure the basic variables in the various projects. For the estimation of standing crop it is recognized that no one sampling strategy is satisfactory for all water bodies, but that comparability can be achieved if the errors associated with a particular strategy are quantified. This applies particularly to the relative efficiency of the chosen collection gear. Any strategy needs to consider not only the problems associated with collection, examination and analysis, but also the limitations set by time, money and manpower. Individual weights and development times are measured more easily and with greater precision than is standing crop. As a result problems of comparability arise not only during collection of data but also during its analysis; significant differ-

TABLE XV. Curvilinear regressions relating duration of egg development (days) to temperature ($^{\circ}\text{C}$).

$$\text{Equation: } \ln D = \ln a + b \ln T + c (\ln T)^2$$

n = number of observations; *c.l.* = confidence limits; *d.f.* = degrees of freedom;
F = variance ratio; *P* = level of significance.

Group	Range (n)	$\ln a$	$b \pm 95\% \text{ c.l.}$	$c \pm 95\% \text{ c.l.}$
Rotifera	0.5 - 25 (88)	2.7547	- 0.2484 ± 0.3341	- 0.2408 ± 0.0861
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Other Cladocera	5 - 30 (55)	2.3279	1.2472 ± 1.1046	- 0.5647 ± 0.2237
All Cladocera	2 - 30 (135)	3.1457	0.4797 ± 0.3935	- 0.4003 ± 0.0817
Calanoida	1 - 31 (121)	3.9650	- 0.4049 ± 0.2738	- 0.1909 ± 0.0625
Cyclopoida	2 - 35 (74)	4.1301	- 0.4141 ± 0.6861	- 0.2159 ± 0.1424
All Copepoda	1 - 35 (195)	3.9673	- 0.3479 ± 0.2700	- 0.2145 ± 0.0593
All Crustacea	1 - 35 (330)	3.7946	- 0.1487 ± 0.2191	- 0.2627 ± 0.0470

ences between similar values being obtained even though residual errors are reduced to very low levels.

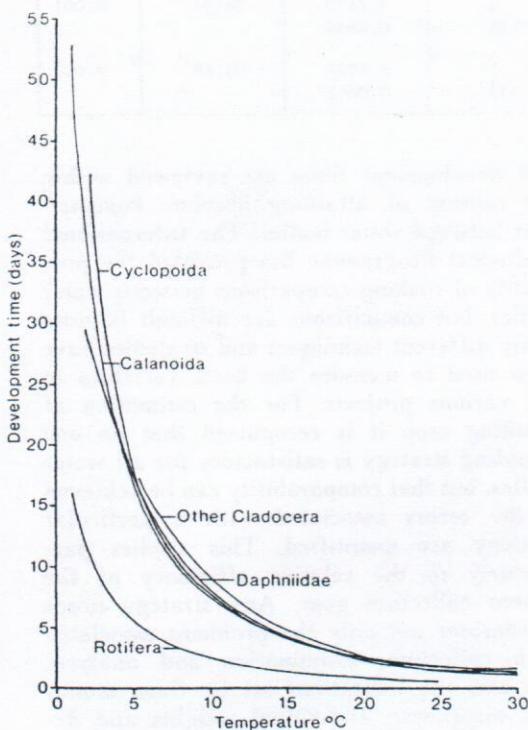


Fig. 15. Duration of egg development for Daphniidae, other Cladocera, Cyclopoida, Calanoida and Rotifera as predicted by the regression equations in Table XIII.

Much in the following recommendations is very obvious and has been repeated many times (e.g. Petrusiewicz & Macfadyen 1969, Edmondson & Winberg 1971). Nevertheless, the Plankton Ecology Group's experience of IBP has shown that it is necessary to restate the importance of estimating variables with confidence limits in order to compare and synthesize zooplankton data from a variety of water bodies.

Standing crop:

1. Define the aims of the investigation, as the appropriate sampling strategy is dependent upon this.
2. Test several collecting tools in the water body being investigated. Rapidly swimming animals require a large, transparent sampler.
3. Whichever tool is chosen, its accuracy and precision has to be determined for studies aiming at absolute comparisons between water bodies.
4. The distribution of samples in space depends upon the nature of the water body and the collecting tool. Irrespective of the nature of the tool, sampling has to be representative for the purpose of absolute comparisons and to encompass the natural variability of zooplankton density both horizontally and vertically. In water bodies of uneven depth, only point sampling is possible, but bulking can reduce the counting load. Integrated sampling is the only solution for very large or very deep water

df	F	P
2; 78	187	0.001
2; 77	1624	0.001
2; 52	329	0.001
2; 132	1420	0.001
2; 118	841	0.001
2; 71	368	0.001
2; 192	1152	0.001
2; 327	2336	0.001

- bodies, but may miss aggregations close to the bottom. Four replicates of the bulked or integrated samples allow a reasonable estimate of the 95% confidence limits of the estimated mean density.
5. Sampling frequency is associated with the generation time of the functionally important and dominant organisms, bearing in mind that this varies with temperature and food conditions.
 6. Errors are involved in the concentration of samples and in subsampling, but both can be reduced to low levels.
 7. Computers and statistics provide powerful analytical tools which do not appear to be used fully. The Plankton Ecology Group hopes to accumulate and, where possible, develop analytical procedures appropriate to plankton samples. There is a great need for statistical expertise in the problems posed by the analysis of plankton data.

Individual weights:

1. Directly measured dry weight gives a good definition of individual size in all groups of planktonic animals. Wet weights and volumes provide a poor basis for predicting dry weight.
2. In most cases the relationship between length and dry weight for crustacean zooplankton can be described with sufficient accuracy and precision by a linear regres-

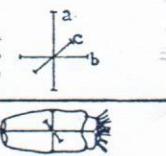
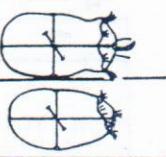
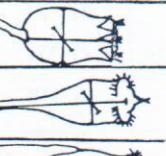
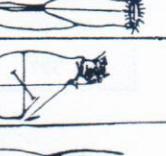
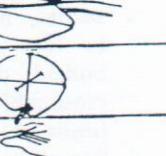
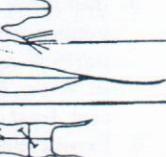
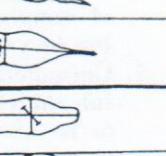
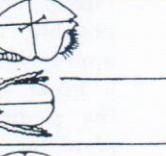
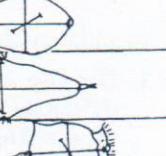
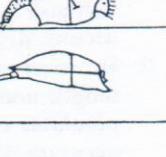
sion on log transformed data. The regression becomes unreliable outside the measured range and the accuracy of the slope is improved by the inclusion of all stages in the life cycle.

3. The length measurement adopted can introduce a discontinuity into the length/weight relationship and it is recommended that spines and appendages are excluded. Length of carapace is an adequate measurement in Cladocera. In Copepoda, total length can be used for nauplii but, for copepodites and adults, the exclusion of the furcal rami or the whole furca may be necessary to ensure continuity in the length/weight relationship.
4. Where possible, the length/weight relationship should be measured for each species but existing regressions for other species or whole genera can be used to predict weight with reasonable accuracy, provided they are accompanied by statistical information. General regressions for Cladocera and Copepoda have proved to be inaccurate and are not recommended.
5. Rotifer species from different localities show a large variation in weight, so each population has to be measured. Dry weights are recommended for rotifers and length/weight regressions may be useful.
6. Formalin-fixation does not seem to affect significantly the dry weight of planktonic animals.

Development times:

1. Whenever possible, development times should be measured for the most abundant species in a water body, and measurements should be made over a wide temperature range. More observations at low temperatures are needed.
2. The type of transformation applied should be determined by the pattern of variation – increasing variation with decreasing temperature suggests a logarithmic transformation.
3. The linear relationship between rate of egg development and temperature is not applicable generally and its future use is to be discouraged. A curvilinear logarithmic relationship appears to be a suitable model for many species.
4. In the absence of detailed development time data for species, a reasonably ac-

Tab. A. FORMULAE FOR CALCULATING VOLUME OF PLANKTON COENOCOES.

Genus	1 Geometric formula used	2 Calculation formula	3 Simplified formula		4 Appendices in % of body volume (b.v.)	Measurements used for formula	5 length = a width = b height = c
			when:	then:			
Anuraeopsis	trilateral truncated pyramid: $\frac{2r_1 h}{3}$	$v = 0,35 \times abc$	$b = 0,5 a; c = 0,1 a;$	$v = 0,05 a^3$	-----	$a = h$ $\frac{bc}{2} = G$	
Ascomorpha	general ellipsoid: $\frac{4\pi \cdot r_1 r_2 r_3}{3}$	$v = 0,52 \times abc$	$b = 0,6 a; c = 0,4 a;$	$v = 0,12 a^3$	-----	$a = 2r_1$ $b = 2r_2$ $c = 2r_3$	
Asplanchna	ellipsoid of revolution $\frac{4\pi \cdot r^2 r_3}{3}$	$v = 0,52 \times ab^2$	$b = c = 0,7 a;$	$v = 0,23 a^3$	-----	$a = 2r_3$ $b = c = 2r$	
Brachionus	general ellipsoid: $\frac{4\pi \cdot r_1 r_2 r_3}{3}$	$v = 0,52 \times abc$	$b = 0,6 a; c = 0,4 a;$	$v = 0,12 a^3$	foot: 10 % of b.v.	$a = 2r_1$ $b = 2r_2$ $c = 2r_3$	
Conochilus	sphere: $\frac{4\pi^3 \cdot \pi}{3}$	$v(\text{col})=4,2a^3$	a:b has to be measured	$v(\text{col})=4,2a^3$	-----	$b = c = 2r$ $a = h$	
individual	cone: $\frac{\pi^2 \cdot \pi \cdot h}{3}$	$v(\text{ind})=0,26ab^2$		$v(\text{ind})=0,26ab^2$			
Collothoea	cone: $\frac{\pi^2 \cdot \pi \cdot h}{3}$	$v = 0,26 \times ab^2$	$a = 7 b;$	$v = 1,8 a^3$	gelatinous hull: 150 - 200 % of b.v.	$b = 2r$ $a = h$	
Euchlanis	1/2 general ellipsoid: $\frac{2\pi \cdot r_1 r_2 r_3}{3}$	$0,52 abc$	$b = 0,6 a$ $c = 0,3 a$	$v = 0,1 a^3$	foot: 5 % of b.v.	$a = 2r_1$ $b = 2r_2$ $c = 2r_3$	
Pilinia	ellipsoid of revolution $\frac{4\pi \cdot r_1 r_2 r_3}{3}$	$0,52 ab^2$	$b = 0,5 a$	$v = 0,13 a^3$	1 % of b.v. x length of petae / length of body (a)	$a = 4r_3$ $b=c=2r_1-2r_2$	
Gastropus	elliptic cylinder: $\pi r_1 r_2 \pi \cdot h$	$0,8 abc$	$b = 0,7 a$ $c = 0,4 a$	$v = 0,20 a^3$	-----	$b = 2r_1$ $c = h$ $a = 2r_2$	
Hexarthra	cone: $\frac{\pi^2 \cdot \pi \cdot h}{3}$	$0,26 ab^2$	$b = 0,75 a$	$v = 0,13 a^3$	33 % of b.v.	$a = h$ $b = c = 2r$	
Kellicottia	cone: $\frac{\pi^2 \cdot \pi \cdot h}{3}$	$0,26 ab^2$	$b = 0,33 a$	$v = 0,05 a^3$	1,5 % of b.v. x caudal+frontal setae / body length	$a = n$ $b = 2r$	
Keratella quadrata-group	parallelepiped: a-b-c	abc	$b = 0,7 a$ $c = 0,33 a$	$v = 0,22 a^3$	5 % of b.v. x caudal spines / body length	a,b,c,	
Keratella cochlearis-group	1/2 cone: $\frac{\pi^2 \cdot \pi \cdot h}{6}$	$0,13 ab^2$	$b = 0,4 a$	$v = 0,02 a^3$	-----	$a = h$ $b = 2r$	
Notholca	segment of ellipsoid: $1/6\pi h(3r_1 r_2 + h^2)$	$0,13(3abc+4c^2)$	$b = 0,4 a$ $c = 0,2 a$	$v = 0,035 a^3$	-----	$a = 2r_1$ $b = 2r_2$ $c = h$	
Plaesoma	general ellipsoid: $\frac{4 \cdot \pi r_1 r_2 r_3 \pi}{3}$	$0,52 abc$	$b = 0,5 a$ $c = 0,4 a$	$v = 0,1 a^3$	hudsoni triacanthum	$a = 2r_1$ $b = 2r_2$ $c = 2r_3$	
			$b = 0,66 a$ $c = 0,66 a$	$v = 0,23 a^3$			
Polyarthra	parallelepiped: a-b-c	abc	$b = 0,7 a$ $c = 0,4 a$	$v = 0,28 a^2$	10 % of b.v.	a,b,c,	
Pompholyx	cylinder: $\pi r^2 \cdot \pi \cdot h$	$0,4 abc$	$b = 0,7 a$ $c = 0,5 a$	$v = 0,15 a^3$	-----	$r^2 \cdot \frac{ab}{4} \cdot \frac{h \cdot c}{2}$	
Synchaeta	cone: $\frac{\pi^2 \cdot \pi \cdot h}{3}$	$0,26 ab^2$	$b = 0,6 a$ $c = 0,6 a$	$v = 0,1 a^3$	-----	$a = h$ $b = 2r$	
Testudinella	cylinder: $\pi r^2 \cdot \pi \cdot h$	$0,4 abc$	$b = a$ $c = 0,2 a$	$v = 0,08 a^3$	foot: 10 % of b.v.	$r^2 \cdot \frac{ab}{4} \cdot \frac{h \cdot c}{2}$	
Trichocerca	cylinder + cone $\pi r^2 \cdot \pi \cdot h + \frac{\pi^2 \cdot \pi \cdot h}{3}$	$0,52 ab^2$	a:b has to be measured in each case	$v = 0,52 ab^2$	0,6 % of b.v. x length of toe / body length	$h = \frac{a}{2}$ $r = \frac{b}{2}$	

curate prediction of egg development time may be obtained using a generalized regression.

5. Areas in which further study is needed, are: (a) the effect of egg size on the duration of egg development; (b) the effect on post-embryonic development of food and temperature considered simultaneously; and (c) determination of food-limiting levels in nature.

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APPENDIX

Proposed formulae for calculating body volume of planktonic rotifers

A. Ruttner-Kolisko (Biological Station Lunz, Austrian Academy of Science, Austria).

Table A (column 1) presents the most appropriate geometric shape and its formula, recommended for calculating the body volume of particular rotifer genera. The measurements used for each formula in Table A (col. 5) are based on the author's own ex-

perience and may have to be revised for particular populations. It is possible to convert this formula into a factor (v) (col. 2) by which body length (a), width (b) and dorso-ventral height (c) must be multiplied to obtain volume. All linear measurements should be taken from living, slightly narcotized adult specimens, not compressed under cover-slip. Newly hatched individuals are half the length of adults. It is essential that the measurements are made on the population being studied, since they vary in different habitats for some species up to 100% and more. Since the linear dimensions are cubed in the calculations, it is advisable that measurements are as accurate as possible.

The relative measurements of length, width and height do not vary greatly within a population, therefore a simplified formula (col. 3) for each species based on its measured length and ratios of width to length and height to length can be used. The ratios proposed in Table A are also based on the author's own experience, and may have to be revised for particular populations. The appendices of some species have been estimated roughly as a percentage of the body volume (b.v.); this is given in Table A (col. 4). As lengths of spines or setae do vary considerably in different species of rotifers, this percentage may have to be modified for a local population by a factor derived from the ratio of appendix length to body length.

It is hoped that the adoption of such formulae and defined factors will lead to comparability of rotifer biomass and production, and to a realistic assessment of the functional role of rotifers in the zooplankton.

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