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Seasonal energy requirements of macrozooplankton from Kosterfjorden, Western Sweden

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Abstract

A study on the macroplankton community in Kosterfjorden, Western Sweden, is used to introduce a term called *Index of population energy-flow*, I_{pef} . This term is defined as the ratio between the energy flow (consumption) through a specific population and the flow through the whole trophic level to which the species belongs. For simplicity, the study is restricted to 6 herbivorous and omnivorous species and 7 carnivorous species. Values for the production, respiration, and excretion are calculated from published data and are presented as means for each of the four seasons. On an annual basis between 8 and 52 % of the assimilated energy is bound in production, between 30 and 85 % is used in respiration, and between 6 and 32 % is excreted. The estimated grazing pressure of the 6 herbivorous/omnivorous species is relatively low compared with the estimated primary production, especially during spring and summer, indicating that most of the primary production goes directly to the benthic community. The copepod *Calanus finmarchicus* has the highest index of population energy-flow among herbivorous/omnivorous species with an annual mean of 87 % and seasonal maximum in autumn ($I_{\text{pef}} = 96 \%$). The copepod *Metridia longa* is most important in spring ($I_{\text{pef}} = 16 \%$) and the three euphausiid species in summer ($I_{\text{pef}} = 4\text{-}5 \%$). Among carnivores the copepod *Chiridius armatus* has the highest annual mean value ($I_{\text{pef}} = 43 \%$) with seasonal maximum in spring ($I_{\text{pef}} = 65 \%$). Small chaetognaths are most important in autumn ($I_{\text{pef}} = 18 \%$) and the polychaete *Tomopteris helgolandica* and the trachymedusa *Aglantha digitale* in winter ($I_{\text{pef}} = 33 \%$ and 17% , respectively).

Introduction

The population of a given species in a community may be seen from several points of view, e.g. as a stock comprising part of the total biota, as a producer of food for a higher trophic level, or as a consumer of food from a lower trophic level. Within each trophic level the impact of each species on the total energy flow through the community is determined by the food consumption of the population. The energy contained in the food is utilized in production, respiration, and excretion, and part of it is not assimilated and is lost in faeces. This makes it possible to calculate food consumption indirectly as:

$$\text{Consumption} = (\text{Production} + \text{Respiration} + \text{Excretion}) / (\text{Assimilation efficiency})$$

The energy transferred by each specific population can then be put in relation to the total transformation of energy in the trophic level. This gives a simple expression of the importance of the species in the energy flow through the community. The Index of population energy-flow, I_{pef} , is thus defined as:

$$I_{\text{pef}_i} = \frac{R_i}{\sum_{j=1}^n R_j} \times 100\% = \frac{(P_i + T_i + U_i)/A_i}{\sum_{j=1}^n (P_j + T_j + U_j)/A_j} \times 100\%$$

where I_{pef_i} denotes Index of population energy-flow of species i , R = consumption, P = production, T = respiration, U = excretion, and A = assimilation efficiency. The summation is taken over all n species belonging to the defined trophic level.

In theory, calculation of species-specific values for I_{pef} requires estimations of production, respiration, excretion, and assimilation efficiency on a population basis to be performed for all n species. In practice, this is impossible, but by restricting the community under study to organisms within a given size range and selecting only the most important species the study becomes feasible.

As an illustration of the community structure seen from the energy-flow point of view, the macrozooplankton community in Kosterfjorden, Western Sweden, is presented. Among the species taken with a 0.4 mm mesh net in Kosterfjorden only 6 herbivorous/omnivorous species and 7 carnivorous species have any considerable influence on the total community energy-flow.

Material and methods

Vertical hauls in triplicate from 200 m depth to the surface were taken regularly in Kosterfjorden, Western Sweden (58°52'N, 11°6'E) with a 1 m diameter conical net, 0.4 mm mesh size, from July 1976 to January 1977, and from April to July 1977. Kosterfjorden has a basin with depth around 200 m, occasionally increasing to about 240 m, and the sampling thus included almost the whole water column. The material was immediately preserved in 4 % borax-buffered formaldehyde-sea water solution and stored until analysed 1 1/2 to 2 years later. The preservation causes losses of body-bound material to some extent (see e.g. OMORI 1978) and the biomass and the biomass-dependent parameters will therefore be somewhat underestimated.

All specimens of large-sized species were removed from the samples, counted, quickly rinsed in distilled water, and dried to constant weight at 60°C. After weighing, the material was incinerated at 500°C for 24 hours and the weight loss, equal to the organic weight, determined. From the remaining material, containing organisms with a dry weight less than about 1 mg, three subsamples were taken for weight determinations and three were taken for identification and counting. The dry weight and organic weight were determined as for the large-sized animals.

The production of each species was estimated by the following technique: Information on weight and age of developmental stages of the different species (sources given in Table 1) was used to construct weight/age relationships for each species. The value for the measured arithmetic mean weight of each species at each sampling occasion was converted to corresponding age by using these relationships. Since the growth curves were usually S-shaped this estimation of the mean individual age in the population will be somewhat biased; dominance of small individuals produces somewhat too high values for the mean age, high proportion of big animals has the opposite effect. For each sampling occasion the population production was calculated as:

Table 1

Sources of data used to estimate the mean individual age in the zooplankton populations

Species	Method of estimating the weight/age relationship
<i>Calanus finmarchicus</i>	Fit by eye from data given by COMITA et al. (1966) and unpublished data from Kosterfjorden
<i>Calanus hyperboreus</i>	No weight/age estimations; assumed $K_2 = 33.3\%$, i.e. $P = (T + U)/2$
<i>Meganyctiphanes norvegica</i>	Length/age from JÖRGENSEN and MATTHEWS (1975), length/weight conversion from BÅMSTEDT (1976)
<i>Thysanoessa inermis</i> <i>Thysanoessa raschii</i>	Length/age from JÖRGENSEN and MATTHEWS (1975), length/weight conversion from MATTHEWS and HESTAD (1977)
<i>Chiridius armatus</i>	Fit by eye from data given by BAKKE and ALVAREZ VALDERHAUG (1978) and unpublished data from Kosterfjorden
<i>Euchaeta norvegica</i>	Fit by eye from data given by BAKKE (1977) and BÅMSTEDT and MATTHEWS (1975)
<i>Eukrohnia hamata</i> <i>Sagitta elegans</i>	Data from SANDS (1980) used to calculate a von Bertalanffy growth curve, length/weight conversion from MATTHEWS and HESTAD (1977)
<i>Sagitta setosa</i>	The same growth curve as used for <i>S. elegans</i>
<i>Tomopteris helgolandica</i>	Unpublished data from Kosterfjorden used to calculate a von Bertalanffy growth curve
<i>Aglantha digitale</i>	Fit by eye from unpublished data from Korsfjorden, western Norway

$$\text{Population production} = \frac{\text{Mean population biomass}}{\text{Mean individual age}}$$

ALLEN (1971) has shown that this is valid if growth is linear in weight or if the mortality is exponential and constant with time. Even if these conditions are not fulfilled mean individual age is better than the widely used parameter mean life span as a base for production estimates (ALLEN 1971). In contrast to the parameter body mass at maturity (BANSE & MOSHER 1980) which is more or less fixed for each population mean individual age varies continuously with the age structure of the population. The latter parameter therefore reflects the variation in growth rate which is associated with shifts in the population from dominance of young, fast-growing to old, slow-growing individuals, and vice versa.

An oversimplification in the estimations was used by assuming that the three herbivorous copepods had zero production from November to February, when primary production is very low.

The production, expressed in organic weight, was converted to energy by using the conversion given by BÅMSTEDT (1981):

$$J/\text{mg dry weight} = 0.2086 (\% \text{ organic matter of dry weight})^{1.0659}$$

From the data given by BÅMSTEDT (1979) the intercept (a) and the regression coefficient (b) for the relationship between respiration rate (T, in $\mu\text{l O}_2 \text{ h}^{-1} \text{ individual}^{-1}$) and dry weight (W, in mg individual^{-1}) expressed by the equation $T = aW^b$ could be obtained. For all species the general regression coefficient $b = 0.803$ (BÅMSTEDT 1979) was used, while species-specific intercept values were calculated as:

$$a = \exp(\ln \bar{T} - 0.803 \ln \bar{W})$$

where \bar{T} and \bar{W} denote average respiration rate and dry weight, respectively, of a given species (from BÅMSTEDT 1979, Table 2).

From the average individual dry weight of each species the corresponding respiration rate could then be calculated by using the specific regression equation. In order to account for higher water-column temperature in summer and autumn (ca. 8°C) than in winter and spring (ca. 5°C) a Q_{10} value of 1.8, previously used for the metabolism of *Calanus finmarchicus* by CORNER et al. (1965), was adopted. The conversion to energy was performed by using the factor $1 \text{ ml O}_2 = 20.9 \text{ J}$ (PARSONS et al. 1977).

Excretion was calculated by using IKEDA's (1974) estimates, assuming a water-column temperature of 8°C for the summer and autumn and 5°C for the winter and spring. These equations are then:

$$\begin{aligned} \text{Summer and autumn:} & \quad U = 0.0889 W^{0.759} \\ \text{Winter and spring:} & \quad U = 0.0730 W^{0.787} \end{aligned}$$

where $U = \mu\text{g N}$ excreted per hour and individual, and $W = \text{mg dry weight per individual}$.

From the average individual dry weight of each species the corresponding excretion rate could then be calculated. The conversion to energy was performed by suggesting that the nitrogen excretion was in the form of ammonium and by using the factor: $1 \text{ mg N} = 24.86 \text{ J}$ (ELLIOT and DAVISON 1975).

Results

The biomass of the plankton community was usually dominated by *Calanus finmarchicus* (Fig. 1) and the large-sized animals, including euphausiids, mysids, amphipods, decapod shrimps, coelenterates, chaetognaths, and tomopterid polychaetes made up on the average only 20% of the total biomass. The seasonal trend included a build-up of biomass during autumn to a maximum in October, and a subsequent continuous decline to minimum level in winter and early spring. The biomass then started to slowly build up again.

Calanus finmarchicus had the highest biomass in autumn and the lowest in spring, while *Metridia longa* and the three euphausiids showed maximum biomass in summer (Fig. 2). Among carnivores, *Chiridius armatus* dominated markedly in spring and summer while in winter several other species showed higher biomasses.

Fig. 3 shows that the productivity of *Calanus finmarchicus* increased from spring to autumn, while that of *Metridia longa* decreased. Decreasing trends were also shown

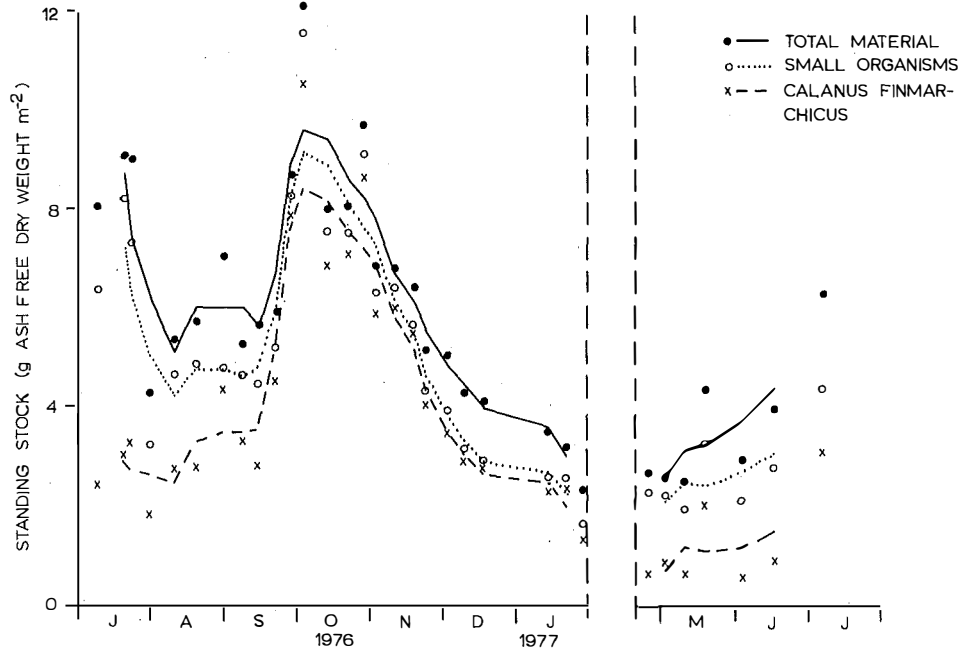


Figure 1

Seasonal succession in standing stock of macrozooplankton in Kosterfjorden. Lines represent moving averages ($n = 3$). The uppermost section represents large-sized animals (approximately > 1 mg dry weight), the middle section "small" animals excluding *Calanus finmarchicus*, which alone is represented by the lower section

by the carnivorous copepods *Chiridius armatus* and *Euchaeta norvegica*. In winter, production was dominated by the polychaete *Tomopteris helgolandica*.

The energy requirements for respiration (Fig. 4) were greatest for *Calanus finmarchicus* in autumn and least in spring. The other dominant herbivores and omnivores usually had highest requirements in summer and least in winter. In spring and summer most of the energy requirements for carnivorous respiration were used by *Chiridius armatus* while in autumn and winter the respiration energy was relatively evenly distributed between the species.

The energy loss through excretion (Fig. 5) showed a similar distribution between species to the respiration loss, with *Calanus finmarchicus* and *Metridia longa* as the most important herbivore/omnivore and *Chiridius armatus* as the most important carnivore.

Table 2 shows the distribution of assimilated energy between the processes of production, respiration, and excretion. The herbivorous/omnivorous copepods used between 26 and 36% for production, i.e. for tissue growth, reproduction and moulting, while slightly more than half of the assimilated energy was used in respiration. The three euphausiid species, on the other hand, had very low production efficiency and more than 80% of the assimilated energy was respired. This is explained by the structure of the populations coming in to Kosterfjorden, which contain mostly old slow-growing individuals.

Table 2

The relative proportion of assimilated energy of different zooplankton populations used for production (P), respiration (T), and excretion (U), calculated on an annual basis

Species	Percentage of assimilated energy used for:		
	P	T	U
Herbivores/omnivores			
<i>Calanus finmarchicus</i>	34	58	8
<i>Calanus hyperboreus</i>	26	54	20
<i>Metridia longa</i>	36	58	6
<i>Meganyctiphanes norvegica</i>	14	80	6
<i>Thysanoessa inermis</i>	9	85	6
<i>Thysanoessa raschii</i>	8	85	7
Carnivores			
<i>Chiridius armatus</i>	41	51	8
<i>Euchaeta norvegica</i>	35	58	7
<i>Eukrohnia hamata</i>	38	30	32
<i>Sagitta elegans</i>	38	52	10
Small chaetognaths	52	40	8
<i>Tomopteris helgolandica</i>	36	55	9
<i>Aglantha digitale</i>	27	58	15

Among carnivorous species between 27 and 52 % of the assimilated energy was bound up in production, the highest value being for the group of small chaetognaths which were dominated by young, fast-growing individuals. Respiration usually accounted for slightly more than 50 % of the assimilated energy, and excretion for another 10 %.

In order to estimate the total energy flow through the community represented by the six herbivorous/omnivorous species and the seven carnivorous species, an assimilation efficiency of 70 % for the former group and 90 % for the latter group has been adopted (see CONOVER 1978 for a review of assimilation efficiencies). The total flow and its species distribution is illustrated in Fig. 6. The food requirements in terms of energy increased from spring to autumn for the herbivores/omnivores but decreased to a minimum in winter. Food requirements of the carnivores decreased instead from spring to autumn and rose again in winter. Another characteristic of the community, clearly demonstrated in Fig. 6, was the extreme dominance of a single species among herbivores/omnivores, while there was more diversity in importance among carnivorous species, especially during autumn and winter.

The Index of population energy-flow has been calculated for the investigated species from the data presented here (Table 3). For herbivores/omnivores the dominant role of *Calanus finmarchicus* in the energy flow is emphasized by its values between 77 and 96 %. *Metridia longa* contributes significantly to the energy flow in spring and summer, the three euphausiid species only during summer.

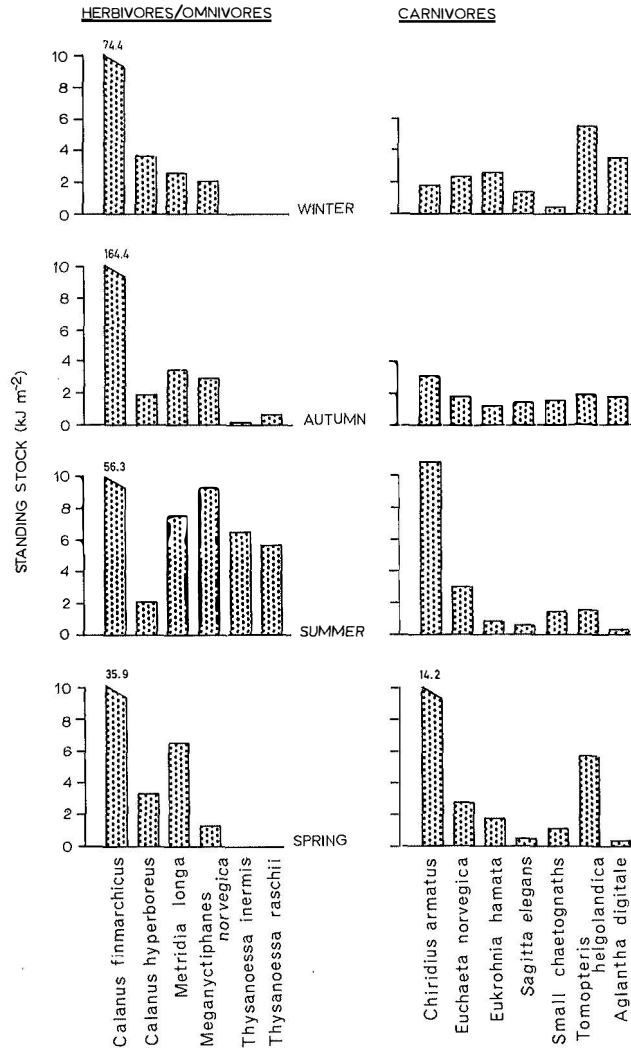


Figure 2

Average seasonal standing stock of dominant zooplankton populations, expressed in energy units. The group "small chaetognaths" include *Eukrohnia hamata* and *Sagitta elegans* with a body length less than 12 mm and all individuals of *S. setosa*.

Among the carnivorous species the population of *Chiridius armatus* transforms more than half of the energy in spring and summer. In autumn small chaetognaths are also very important and in wintertime the trachymedusa *Aglantha digitale* and especially the polychaete *Tomopteris helgolandica* are key organisms in the energy flow through this trophic level.

A ranking of the species on an annual basis can be made from data on the Index of population energy-flow in Table 3. Among herbivores/omnivores *Calanus finmarchicus* gets an index value of 87 %, *Metridia longa* 8 %, *Meganyctiphanes norvegica* 2 %, *Thysanoessa inermis* 1 %, and *Thysanoessa raschii* 1 %.

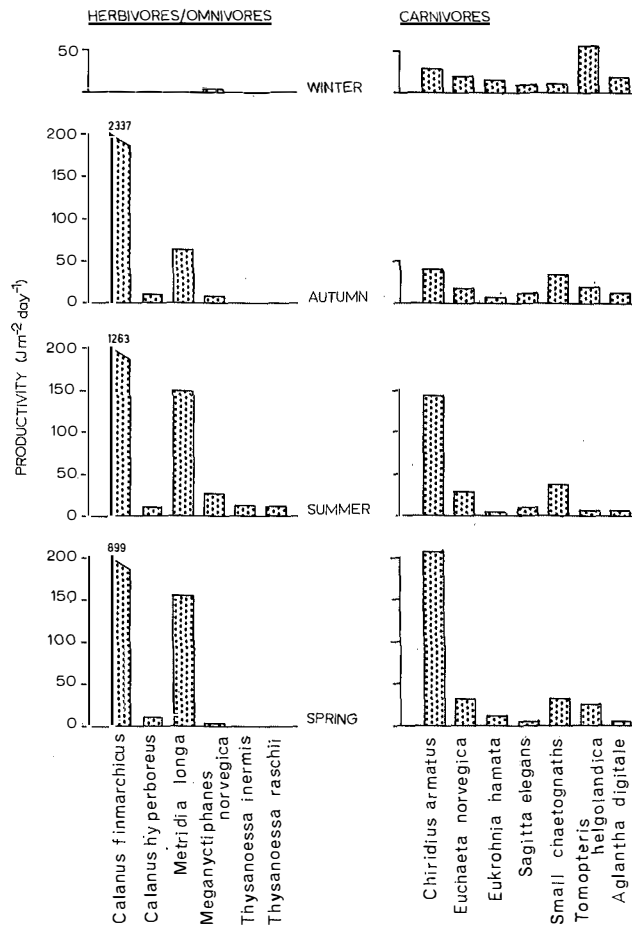


Figure 3

Average seasonal productivity of dominant zooplankton populations, expressed in energy units.

and the other three species 1% each. Corresponding ranking of the carnivores gives: *Chiridius armatus* 43%, *Tomopteris helgolandica* 15%, *Euchaeta norvegica* 13%, small chaetognaths 11%, *Aglantha digitale* 8%, *Eukrohnia hamata* and *Sagitta elegans* 5% each.

Discussion

Data on the primary productivity in northern latitudes have been reviewed by MATTHEWS and HEIMDAL (1980). By using the conversion: 1 mg carbon = 47.7 J (PLATT and IRWIN 1973), the average daily primary production amounts roughly to 90 kJ m⁻² in spring, 60 kJ in summer, 20 kJ in autumn, and 5 kJ in winter. If these values are representative for Kosterfjorden it means that about 3% of the primary production is used by macroplanktonic herbivores in spring, 9% in summer, 60% in autumn, and 45% in winter. This, in turn, suggests that most of the primary production is transformed directly down to the benthic community, especially during spring and summer.

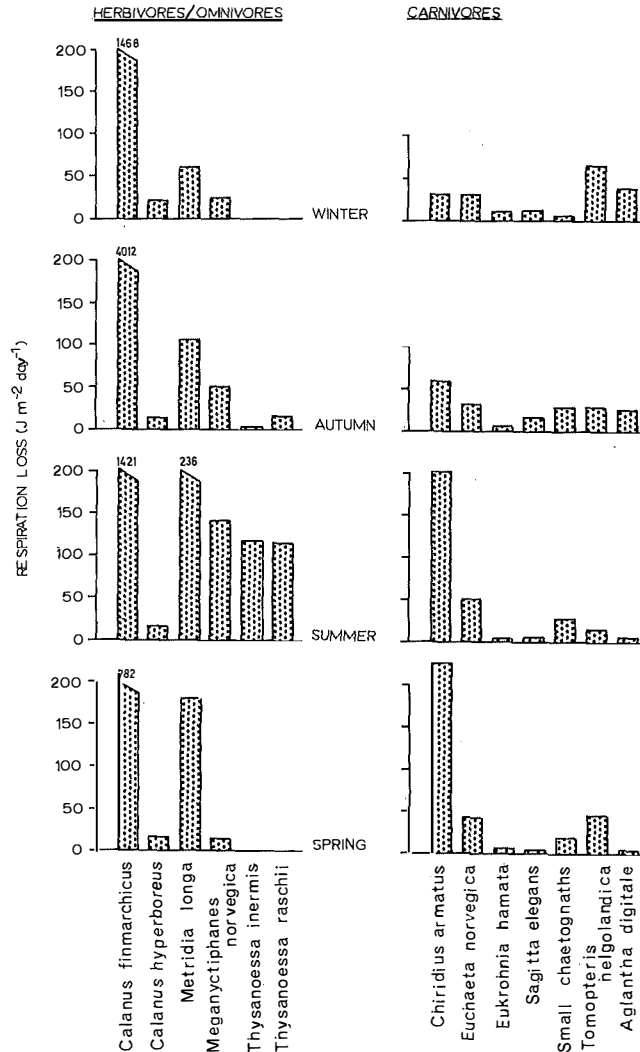
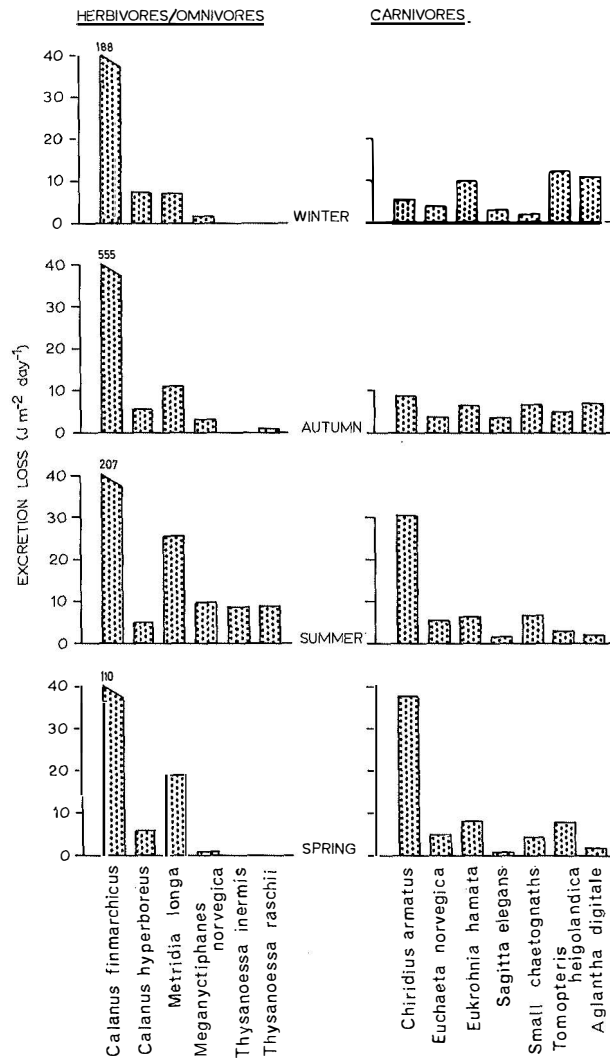


Figure 4

Average seasonal respiration loss of dominant zooplankton populations, expressed in energy units

The estimated annual energy requirement of the carnivorous species is ca. 210 kJ m⁻² and the production of the three herbivorous/omnivorous copepods, which are possible prey for these carnivores, is estimated at about 450 kJ m⁻². Since many other, smaller species probably contribute considerably to the diet of the carnivorous species, a main part of the herbivore production can be consumed by other predators than those discussed here.

The Index of population energy-flow gives a simple numerical expression of the importance of a given species in its trophic position. This is useful when one has to restrict an investigation to only the most important part of a community. In Kosterfjorden, for example, one can get a very good picture of the large primary

**Figure 5**

Average seasonal excretion loss of dominant zooplankton populations, expressed in energy units

consumers by only studying *Calanus finmarchicus* since this population controls almost 90% of the energy flow. Similarly, a restriction to the three or four most important carnivorous species makes it possible to estimate 3/4 of the energy flow through that trophic level. Ideally, however, a study concerning the energy flow through a community should include the whole size range of organisms, from ciliates to large jellyfishes. This is more obvious when considering the strong influence of body size on the production and metabolic activity of the organisms. Such a study would require quite a different amount of work. Although microzooplankton have been included as part of the total community in some recent studies (e.g. ERIKSSON et al. 1977) lack of data on production, respiration, excretion, and assimilation makes it difficult to include

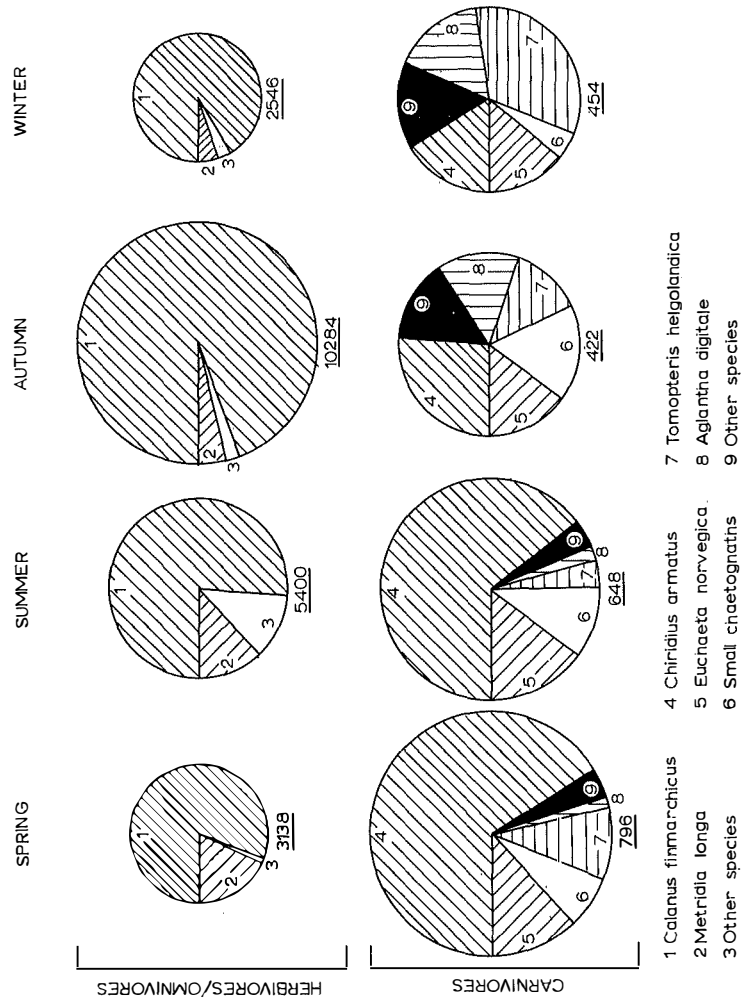


Figure 6

Average seasonal energy requirements per day for herbivores/omnivores and carnivores, respectively, and the species distribution of these requirements. Underlined values give the total daily energy requirements in J m^{-2} . Scales for the circles are different for herbivores/omnivores and carnivores

them in energy-flow studies. A study of the ecological energetics of a plankton community, carried out synoptically on both micro-, and megaplankton is therefore greatly needed. Even with information from such an investigation we must accept, however, that most of the details of the pathways of energy flow will be hidden, since the relationships between species and their flexibility in nature are largely unknown.

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Table 3

Average seasonal *Index of population energy-flow*, I_{pef} , of various zooplankton populations

Species	Index of population energy-flow			
	Spring	Summer	Autumn	Winter
Herbivores/omnivores				
<i>Calanus finmarchicus</i>	81.5	76.5	95.9	92.9
<i>Calanus hyperboreus</i>	1.5	0.8	0.4	1.6
<i>Metridia longa</i>	16.1	10.8	2.5	3.8
<i>Meganyctiphanes norvegica</i>	0.8	4.7	0.8	1.7
<i>Thysanoessa inermis</i>	0	3.7	0.1	0
<i>Thysanoessa raschii</i>	0	3.6	0.3	0
Carnivores				
<i>Chiridius armatus</i>	65.4	63.7	28.2	15.7
<i>Euchaeta norvegica</i>	10.8	13.8	14.0	13.3
<i>Eukrohnia hamata</i>	3.2	2.3	5.0	8.9
<i>Sagitta elegans</i>	1.1	2.2	8.7	7.6
Small chaetognaths	7.5	11.6	18.2	4.8
<i>Tomopteris helgolandica</i>	10.6	4.1	13.8	33.0
<i>Aglantha digitale</i>	1.3	2.2	12.2	16.7

References

- ALLEN, K. R., 1971. Relation between production and biomass. J. Fish. Res. Bd. Canada **28**, 1573–1581.
- BAKKE, J. L. W., 1977. Ecological studies on the deep-water pelagic community of Korsfjorden, western Norway. Population dynamics of *Euchaeta norvegica* (Crustacea, Copepoda) from 1971 to 1974. *Sarsia* **63**, 49–55.
- BAKKE, J. L. W. and V. ALVAREZ VALDERHAUG, 1978. Ecological studies on the deep-water, pelagic community of Korsfjorden, western Norway. Population biology, biomass and caloric content of *Chiridius armatus* (Crustacea, Copepoda). *Sarsia* **63**, 247–254.
- BÅMSTEDT, U., 1976. Studies on the deep-water pelagic community of Korsfjorden, western Norway. Changes in the size and biochemical composition of *Meganyctiphanes norvegica* (Euphausiacea) in relation to its life cycle. *Sarsia* **61**, 15–30.
- BÅMSTEDT, U., 1979. Seasonal variation in the respiratory rate and ETS activity of deep-water zooplankton from the Swedish west coast. In: E. Naylor and R. G. Hartnoll (eds). *Cyclic phenomena in marine plants and animals*, 267–274. Pergamon Press, Oxford.
- BÅMSTEDT, U., 1981. Water and organic content of boreal macrozooplankton and their significance for the energy content. *Sarsia* **66**, 59–66.
- BÅMSTEDT, U. and J. B. L. MATTHEWS, 1975. Studies of the deep-water pelagic community of Korsfjorden, western Norway. The weight and biochemical composition

- of *Euchaeta norvegica* Boeck in relation to its life cycle. In: H. Barnes (ed.), Proc. 9th Europ. mar. biol. Symp., 311–327. Aberd. Univ. Press Ltd.
- BANSE K. and S. MOSHER, 1980. Adult body mass and annual production/biomass relationships of field populations. Ecological Monographs **50**, 355–379.
- COMITA, G. W., S. M. MARSHALL and A. P. ORR, 1966. On the biology of *Calanus finmarchicus*. XIII. Seasonal change in weight, calorific value and organic matter. J. Mar. Biol. Ass. U.K. **46**, 1–17.
- CONOVER, R. J. 1978. Transformation of organic matter. In: O. Kinne (ed.), Marine Ecology. TV. Dynamics, 221–499. John Wiley & Sons, Chichester.
- CORNER, E. D. S., C. B. COWEY and S. M. MARSHALL, 1965. On the nutrition and metabolism of zooplankton. III. Nitrogen excretion by *Calanus*. J. Mar. Biol. Ass. U.K. **45**, 429–442.
- ELLIOT, J. M. and W. DAVISON, 1975. Energy equivalents of oxygen consumption in animal energetics. Oecologia (Berl.) **19**, 195–201.
- ERIKSSON, S., C. SELLEI and WALLSTRÖM, 1977. The structure of the plankton community of the Öregrundsgrepen (southwest Botnian Sea). Helgol. Wiss. Meeresunters. **38**, 582–597.
- IKEDA, T., 1974. Nutritional ecology of marine zooplankton. Mem. Fac. Fish., Hokkaido Univ. **22**, 1–97.
- JÖRGENSEN, G. and J. B. L. MATTHEWS, 1975. Ecological studies on the deep-water pelagic community of Korsfjorden, western Norway. Population dynamics of six species of euphausiids in 1968 and 1969. Sarsia **59**, 67–84.
- MATTHEWS, J. B. L. and B. R. HEIMDAL, 1980. Pelagic productivity and food chains in fjord systems. In: H. J. Freeland, D. Farmer and C. D. Levings (eds), Proc. Fjord Oceanography Workshop Sidney, B. C. June 1979. NATO Conference Series IV: Marine Science, 377–398. Plenum Publ. Corp. N.Y.
- MATTHEWS, J. B. L. and L. HESTAD, 1977. Ecological studies on the deep-water pelagic community of Korsfjorden, western Norway. Length/weight relationships for some macroplanktonic organisms. Sarsia **63**, 57–63.
- OMORI, M., 1978. Some factors affecting on dry weight, organic weight and concentration of carbon and nitrogen in freshly prepared and in preserved zooplankton. Int. Revue ges. Hydrobiol. **63**, 261–269.
- PARSONS, T. R., M. TAKAHASHI and B. HARGRAVE, 1977. Biological Oceanographic Processes. Pergamon Press, Oxford.
- PLATT, T. and B. IRWIN, 1973. Caloric content of phytoplankton. Limnol. Oceanogr. **18**, 306–310.
- SANDS, N. J., 1980. Ecological studies on the deep-water pelagic community of Korsfjorden, western Norway. Population dynamics of the chaetognaths from 1971–1974. Sarsia **65**, 1–12.