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RNA concentration of zooplankton: Relationship with size and growth[1]

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Abstract

The relationship between RNA concentration and dry weight (W) of zooplankton from the Korsfjord, western Norway, was best described by a power function, $[RNA] = aW^b$. Dry weight explained about 75% of the intraspecific and 43% of the interspecific variation in RNA concentration. The intraspecific regression slope (average −0.74) was significantly steeper than the multispecific slope (−0.33). Published data on growth rate of zooplankton from Korsfjorden and other areas revealed a pattern with dry weight similar to that for RNA concentration, with an interspecific regression slope of −0.32. Combining the interspecific regressions of growth rate and RNA concentration vs. dry weight gives a relationship between growth rate (k, coefficient of daily exponential growth) and RNA concentration ($\mu g \cdot mg$ dry wt^{-1}), $k \cdot 10^3 = 0.795 \times [RNA]$, which can be used to estimate the average growth rate of macrozooplankton samples with RNA concentrations between 3 and 70 $\mu g \cdot mg$ dry wt^{-1}.

A mixed zooplankton sample may seasonally consist of a wide variety of sizes of animals that are not growing, or it may consist of almost uniformly sized animals with widely varying growth rates. Size analysis and use of a theoretical relationship between size and growth does not, therefore, give a correct picture of production. The RNA/growth-rate relationship may, in such situations, be a useful instrument for estimating secondary production.

A positive correlation between RNA concentration and growth rate has been demonstrated for many organisms of widely different taxa (Sutcliffe 1970). Sutcliffe (1965) described the relationship between RNA concentration and growth rate for the amphipod *Orchestia platensis* and used this to predict the growth rates of the brine shrimp *Artemia salina* and the gastropod *Nassarius obsoletus*. Similar relationships have been described for the copepods *Euchaeta elongata* (Dagg and Littlepage 1972) and *Euchaeta norvegica* (Båmstedt and Skjoldal 1976) and for the euphausiid shrimp *Meganyctiphanes norvegica* (Skjoldal and Båmstedt 1976). Comparison of these relationships (Fig. 1) shows pronounced differences, suggesting that a general relationship would have little predictive value for mixed zooplankton samples. However, one should be cautious not to base hasty conclusions concerning the usefulness of RNA on these data.

The relationship for *O. platensis* (Sutcliffe 1965) deviates from the others in predicting much higher growth rates for low concentrations of RNA. This discrepancy is mainly due to much lower estimates of RNA concentration in the fast-growing tropical amphipod (Sutcliffe 1965: fig. 5) than in zooplankton species of similar size from boreal regions (as described here). The relationship for *A. salina* is a linear regression of a scattered plot of growth rates vs. RNA concentrations from a series of experiments where feeding varied drastically (Dagg and Littlepage 1972: fig. 4). The remaining three relationships were obtained by comparing, more or less indirectly, measured RNA contents with estimates of growth

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rates and are subject to the errors and uncertainties of studies of population dynamics. The relationship for *E. elongata* (Dagg and Littlepage 1972) differed significantly from those for *E. norvegica* and *M. norvegica*, which were not significantly different from each other.

Previous work on the relationship between RNA concentration and growth rate does not therefore conclusively eliminate the possibility of using RNA as an estimate of growth rate of mixed populations. Pease (1968) and Dagg and Littlepage (1972) clearly showed that RNA content poorly reflected changes in growth rate caused by widely varying feeding conditions. Since studies on population dynamics often yield a fairly steady and consistent growth pattern during the productive period of the year, the feeding condition of natural populations may be regarded as rather stable, at least during that period. In the Korsfjord this is indicated by high standing stocks of herbivores, omnivores, and carnivores from spring to early winter (Matthews and Bakke 1977).

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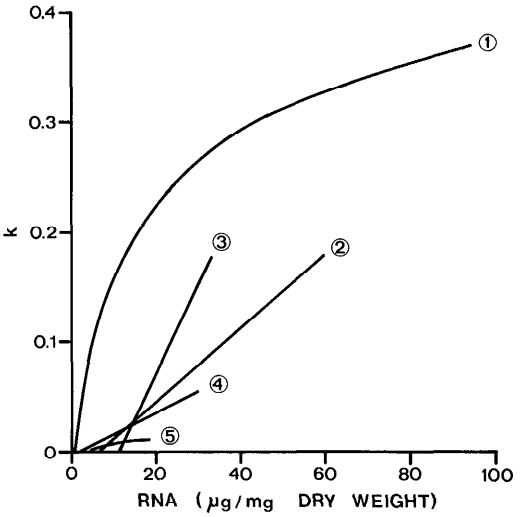

Fig. 1. Five reported intraspecific relationships between growth rate and RNA concentration. 1—*Orchestia platensis* (Sutcliffe 1965); 2—*Artemia salina* (Dagg and Littlepage 1972); 3—*Euchaeta elongata* (Dagg and Littlepage 1972); 4—*Euchaeta norvegica* (Båmstedt and Skjoldal 1976); 5—*Meganyctiphanes norvegica* (Skjoldal and Båmstedt 1976).

Material and methods

Samples of living zooplankton were collected by oblique hauls with a Beyer's low-speed midwater trawl (0.9-mm mesh) from about 500-m depth to the surface in the Korsfjord, western Norway (60°12′N, 05°14′E). The animals from the closed cod end were immediately transferred to containers of seawater at 6°–8°C—the temperature at intermediate depths in the fjord (Bakke and Sands 1977). Preliminary sorting was carried out at sea and further sorting for species, sex, and stage in the laboratory. The sorted animals were kept in containers in the dark at 6°C for about 20 h. Single animals were collected with a small sieve and forceps, quickly rinsed in distilled water, dropped into liquid nitrogen, and kept at −26°C until freeze-dried between 4 h and 2 days later. The freeze-dried animals were then kept desiccated at −26°C for 1 to 3 days and thereafter weighed to the nearest 0.01 mg.

The analytical samples for RNA determination consisted of single specimens for the species *M. norvegica, Boreomysis arctica, Parathemisto abyssorum, Pasiphaea tarda, Pasiphaea multidentata, Tomopteris helgolandica,* and *Dimophyes arctica.* Samples of copepods consisted of either 5 or 10 individuals and the samples of the other eight species had between 2 and 30 specimens. Care was always taken to select individuals of uniform size in the pooled samples.

The analytical samples of freeze-dried animals were homogenized in ice-cold distilled water, and 4.0 ml of the homogenate was mixed with 2.0 ml of 0.6 N perchloric acid. Our procedure for separation and determination of RNA was that of Dagg and Littlepage (1972); the samples were always kept on ice. Centrifugation at 3,000–4,000 *g* was done in a re-

Table 1. Intra- and multispecific relationships between RNA concentration and body dry weight (W) described by least-squares regression equation [RNA] = aW^b for zooplankton collected in Korsfjord on seven sampling occasions over 13-month period. n denotes number of determinations; L_1 and L_2 denote lower and upper 95% confidence limits of regression slope (b). Values for eggs have been excluded in regression analyses and are shown in parentheses.

			Range		Regression equation				
	Sex/Stage	n	Dry wt (mg)	RNA concn ($\mu g \cdot mg$ dry wt^{-1})	a	b	L_1	L_2	r
			27 February 1974						
Total (7 species)		59	0.3–118.8	2.5–40.5	17.85	−0.23	−0.32	−0.15	−0.58*
Chiridius armatus	c-VI ♀♀	1	0.6	40.5					
Euchaeta norvegica	c-VI ♀♀	4	2.4–2.9	6.8–9.7					
Metridia longa	c-VI mixed	1	0.3	31.6					
Meganyctiphanes norvegica	mixed	45	17.2–118.8	2.5–20.8	37.89	−0.43	−0.55	−0.32	−0.76*
Pasiphaea tarda	♀	1	—	5.4					
(*P. tarda*)	(egg)	(3)	(4.0–4.3)	(2.8–4.1)					
Eukrohnia hamata	mixed	5	2.8–8.8	6.4–14.2	15.43	−0.73	−1.76	0.30	−0.53†
Aglantha digitale	mixed	2	4.8–6.3	5.5–6.4					
(*Argentina* sp.)	(egg)	(1)	(2.6)	(15.8)					
			30 April 1974						
Total (12 species)		109	0.2–163.1	3.4–68.0	21.66	−0.33	−0.37	−0.29	−0.84*
Calanus finmarchicus	c-V,c-VI	8	0.5–0.9	12.7–56.2	14.63	−1.96	−3.41	−0.51	−0.79‡
Chiridius armatus	c-VI ♀♀	7	0.5–0.8	11.7–46.4	19.36	0.08	−5.08	5.24	0.02†
Euchaeta norvegica	c-IV,V,VI	20	0.2–2.7	9.4–52.4	18.30	−0.70	−0.80	−0.60	−0.96*
Metridia longa	c-VI mixed	5	0.2–0.4	35.3–68.0	17.20	−0.94	−3.31	1.43	−0.54†
Meganyctiphanes norvegica	mixed	10	11.7–31.9	5.9–15.1	44.13	−0.52	0.92	−0.11	−0.70§
Boreomysis arctica	mixed	25	4.6–15.0	5.3–17.5	44.55	−0.70	−0.97	−0.43	−0.74*
Hemimysis abyssicola	adults	5	2.1–3.2	7.6–13.8	31.19	−1.18	−2.00	−0.36	−0.91‡
Pasiphaea multidentata	mixed	11	27.8–163.1	3.4–9.2	36.37	−0.41	−0.59	−0.24	−0.85*
Pontophilus norvegicus	zoea	2	1.6–2.0	16.7–18.9					
Parathemisto abyssorum	adults	3	3.7–4.7	19.7–23.6					
Eukrohnia hamata	mixed	7	1.7–5.9	9.0–23.7	36.53	−0.74	−1.21	−0.27	−0.86‡
Tomopteris helgolandica	mixed	5	4.0–8.8	8.2–16.7	69.89	−0.98	−1.17	−0.79	−0.97§
			27 May 1974						
Total (4 species)		40	0.3–71.3	3.0–20.7	10.52	−0.20	−0.28	−0.12	−0.64*
Euchaeta norvegica	c-IV,V,VI	20	0.3–5.0	3.0–17.2	9.47	−0.62	−0.71	−0.53	−0.96*
Meganyctiphanes norvegica	mixed	7	23.0–71.3	4.8–8.5	26.76	−0.41	−0.61	−0.20	−0.85‡
Pontophilus norvegicus	zoea	5	1.8–2.9	14.6–20.7	28.39	−0.66	−1.53	0.21	−0.87†
Munida sp.	zoea	8	0.6–0.7	10.0–13.4	10.16	−0.29	−1.62	1.03	−0.18†

Table 1. Continued.

	Sex/Stage	n	Range: Dry wt (mg)	Range: RNA concn (μg·mg dry wt⁻¹)	Regression equation: a	b	L_1	L_2	r
			9 July 1974						
Total (2 species)		44	0.6–101.7	3.3–26.2	9.00	−0.18	−0.23	−0.13	−0.72*
Euchaeta norvegica	c-V,VI	25	0.6–4.3	4.2–26.2	12.63	−0.79	−0.99	−0.59	−0.86*
Meganyctiphanes norvegica	mixed	19	9.0–101.7	3.3–12.7	36.54	−0.51	−0.60	−0.42	−0.94*
			19 September 1974						
Total (11 species)		58	0.4–155.0	3.2–22.3	10.55	−0.16	−0.24	−0.08	−0.47*
Calanus finmarchicus	c-VI	1	0.5	18.1					
Calanus hyperboreus	c-V,VI	4	1.1–2.2	5.7–11.8					
Chiridius armatus	c-VI ♀♀	5	0.8–0.9	10.7–18.6	8.58	−2.43	−7.91	3.05	−0.59†
Euchaeta norvegica	c-V,VI	15	1.3–4.3	3.8–11.2	14.28	−0.83	−0.99	−0.66	−0.96*
(*E. norvegica*)	(eggsac)	(4)	(1.1–1.2)	(16.4–21.0)					
Meganyctiphanes norvegica	mixed	10	14.8–155.0	3.8–21.3	64.60	−0.57	−0.80	−0.35	−0.89*
Thysanoessa sp.	mixed	4	2.2–9.6	6.9–16.7					
Boreomysis arctica	mixed	6	5.0–25.2	4.4–22.3	119.65	−1.02	−1.22	−0.81	−0.99*
Parathemisto abyssorum	mixed	2	5.9–14.2	16.1–17.7					
Eukrohnia hamata	mixed	4	3.3–8.3	7.9–15.0					
Aglantha digitale	mixed	4	5.4–14.0	3.8–7.8					
Dimophyes arctica	mixed	3	6.8–12.4	3.5–9.2					
			10 December 1974						
Total (2 species)		27	0.7–142.5	1.8–14.6	6.14	−0.11	−0.20	−0.02	−0.43‡
Euchaeta norvegica	c-V,VI	19	0.7–5.6	3.5–8.9	7.07	−0.43	−0.55	−0.32	−0.88§
Meganyctiphanes norvegica	mixed	8	10.0–142.5	1.8–12.6	19.51	−0.43	−0.84	−0.03	−0.71†
			27 February 1975						
Total (2 species)		36	0.7–161.0	3.7–20.5	9.45	−0.20	−0.27	−0.13	−0.69*
Euchaeta norvegica	c-V,VI	16	0.7–4.3	3.7–20.5	14.01	−0.94	−1.60	−0.28	−0.98*
(*E. norvegica*)	(eggsac)	(4)	(1.0–1.1)	(17.0–27.5)					
Meganyctiphanes norvegica	mixed	20	7.6–161.0	3.7–9.6	11.38	−0.23	−0.34	−0.12	−0.71*

* $P \leq 0.001$.
† Not significant ($P \geq 0.05$).
‡ $0.05 > P > 0.01$.
§ $0.01 > P > 0.001$.

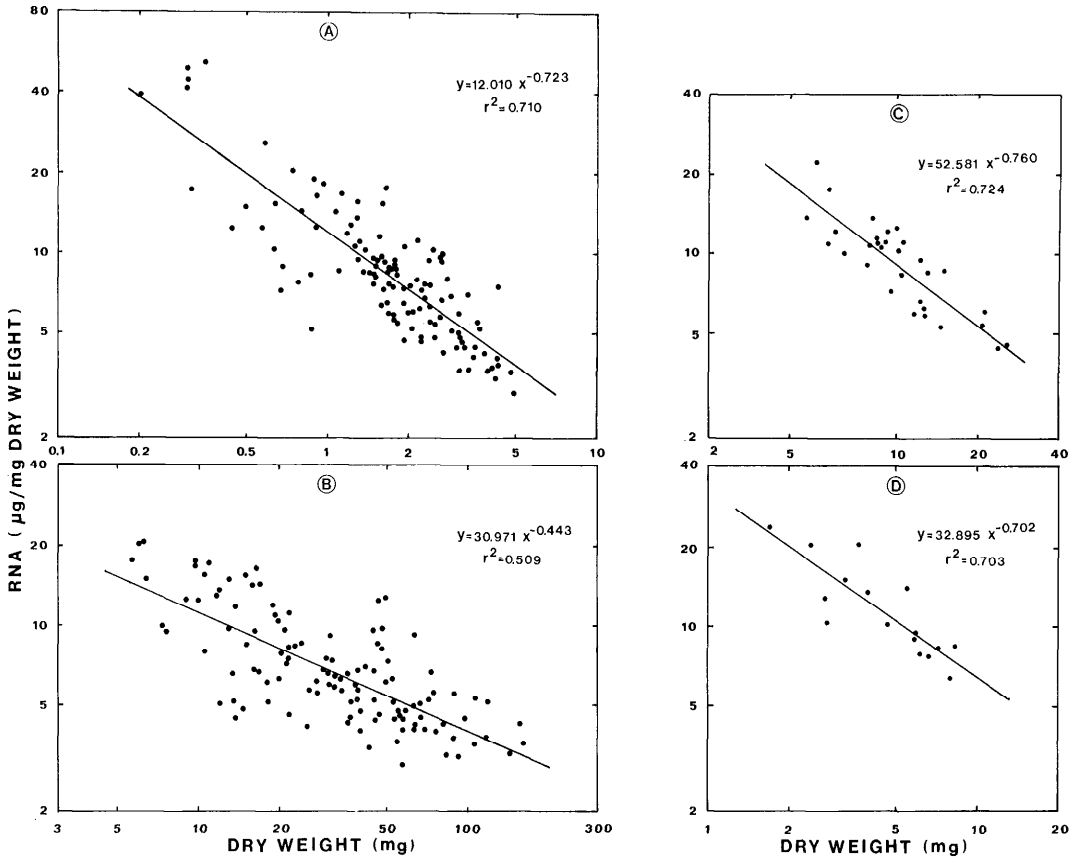

Fig. 2. Relationships (least-squares regression) between RNA concentration and dry weight for four zooplankton species from Korsfjord. A—*Euchaeta norvegica*; B—*Meganyctiphanes norvegica*; C—*Boreomysis arctica*; D—*Eukrohnia hamata*. Points represent individual determinations on various sampling occasions over 13-month period. Table 1 gives information on sampling frequencies for species.

frigerated centrifuge. Analysis of protein in the RNA extract indicated negligible quantities both by a Lowry-protein check (Lowry et al. 1951) on one occasion and by comparing the absorbances at 260 and 280 nm (Munro and Fleck 1966) on several occasions.

Results

A summary of our results is presented in Table 1. There was commonly a negative relationship between RNA concentration and individual dry weight (W). The regression equation used was of the form [RNA] = aW^b, which almost invariably provided a better fit than a semilogarithmic relationship ([RNA] = ae^{bW}). The correlation was usually highly significant and the regression most often explained more than 60% (average 75%) of the total intraspecific variation in RNA concentration; the exceptions were species where animals in only a narrow size range were included or few determinations were performed.

The size dependence of RNA concentration masked any seasonal variation. Figure 2 gives plots of RNA concentration vs. individual dry weight for the copepod *E. norvegica*, the euphausiid shrimp *M. norvegica*, the mysid shrimp *B. arctica*, and the chaetognath *Eukrohnia hamata* on all sampling occasions. The coefficients of determination (r^2) indicate that from 51 to 72% of the variation in

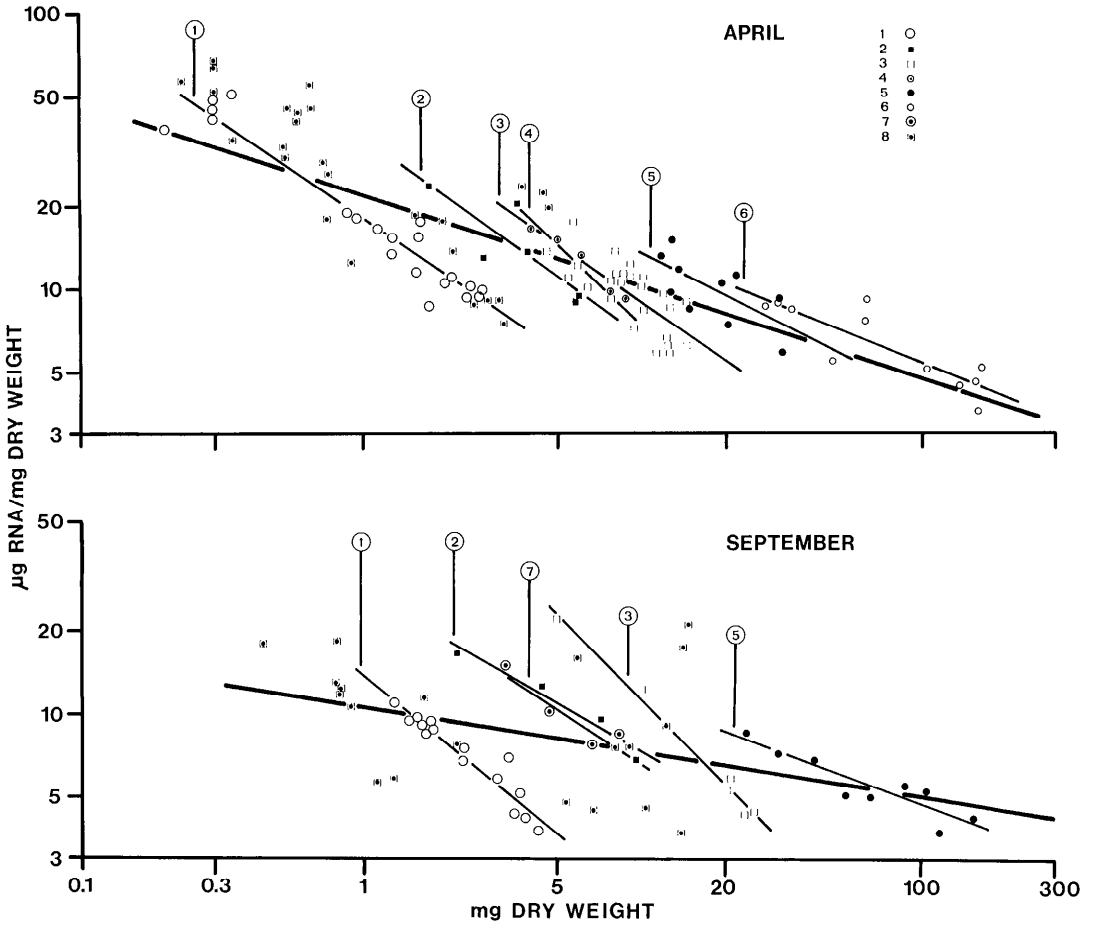

Fig. 3. Relationship (least-squares regression) between RNA concentration and dry weight for separate zooplankton species (thin lines) and total material (heavy lines) collected in Korsfjord, April and September 1974. Numerals identify species. 1—*Euchaeta norvegica*; 2—*Eukrohnia hamata*; 3—*Boreomysis arctica*; 4—*Tomopteris helgolandica*; 5—*Meganyctiphanes norvegica*; 6—*Pasiphaea multidentata*; 7—*Thysanoessa* sp.; 8—remaining species included in total material.

RNA concentration was explained by the variation in dry weight.

The regression slopes for the single species were generally significantly steeper than that for the combined material examined on each sampling occasion (Table 1), with an average slope of −0.74 (SD = 0.51, n = 26). This is illustrated in Fig. 3 for the two occasions (April and September 1974) when the greatest number of species was investigated. The regression lines for the separate species are displaced more or less parallel to each other along the regression line for the total data. Two individuals of the same size, a juvenile of a big species and an adult of a small species, will thus have different amounts of RNA. An analysis of covariance showed that none of the specific regression lines in April was significantly different, and the slope that fitted all six regressions best was −0.73. In September the same test indicated significant differences between some of the slopes of the five specific regression lines; a multiple-range test showed *B. arctica* to be significantly different from the others at $P < 0.05$.

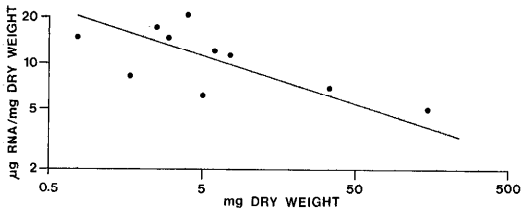

Fig. 4. Relationship (geometric mean functional regression) between RNA concentration and average individual dry weight of nine zooplankton species (cf. Table 2). Regression equation: [RNA] = $18.611 \times \bar{W}^{-0.315}$.

The regression intercept (a, Table 1) for *E. norvegica* and *M. norvegica*—the two species that were analyzed on every occasion—varied significantly ($P < 0.0005$) during the study period. The regression slopes (b, Table 1), on the other hand, did not vary significantly, and the slopes best fitting all regression lines were −0.68 for *E. norvegica* and −0.44 for *M. norvegica*. These results indicate that the RNA concentration changes proportionally during the season in individuals of different sizes. The highest concentrations of RNA were generally found during spring (April, Table 1).

The regression slopes for the combined material on the various dates (Table 1) are significantly different from each other (F-test, $P < 0.0005$). This could be partly due to different species in the material. For all the data combined, excluding the data for eggs of *E. norvegica* (weights of single eggs were not determined), the regression equation was [RNA] = $13.286\ W^{-0.229}$, with a coefficient of determination of 0.37.

Discussion

RNA vs. dry weight—The strict intraspecific negative relationships between RNA concentration and individual dry weight (*see Figs. 2 and 3, Table 1*) agree well with most previous findings for marine animals (Sutcliffe 1965; Dagg and Littlepage 1972; Regnault and Luquet 1974). Baudouin and Scoppa (1975) found similar RNA concentrations in different-sized individuals of *Daphnia hyalina* and explained their findings by stating that the growth rate of *D. hyalina* was constant throughout life; their fig. 2 suggests, however, that the weight-specific growth rate decreased markedly.

There are some reports indicating that the negative relationship between RNA concentration and weight may not hold for early juvenile stages. Pease (1968) found an increasing RNA concentration during the first larval stages of *A. salina* and *Euphausia pacifica*. This has also been reported for some insects (e.g. Church and Robertson 1966). Sulkin et al. (1975) found no correlation between the RNA concentration and fresh weight of the zoea larvae of the crab *Rhithropanopeus harrisii*, but the RNA:DNA ratio showed a cyclic pattern correlated with the moulting cycle.

The inverse relation between RNA concentration and weight of the species (Table 1, Fig. 3) also agrees with previous observations on the RNA content of various arthropods (e.g. Barnes et al. 1963; Devi et al. 1963; Lang et al. 1965; Church and Robertson 1966; Vickers and Mitlin 1966; Chandran and Michael 1968; Baudouin and Scoppa 1975). For mammals, an inverse relationship between body weight and RNA concentration of liver and muscle has been demonstrated (Munro and Downie 1964; Munro and Gray 1969).

The multispecific regression for all the data combined explained only 37% of the total variation in RNA concentration. This is, however, mainly due to the steeper intraspecific relationships (Fig. 3). The data were obtained from individuals whose weight ranges represented a somewhat variable fraction in the upper part of the total weight ranges for the separate species. For the purpose of comparison with an interspecific regression for growth rate against dry weight (discussed below), we tried a procedure to eliminate intraspecific variation. For each species analyzed over a wide size range, the relationship between individual dry weight and RNA concentration was determined with good precision (Table 2). The average individual weight, $\bar{W} = (W_o + W_t)/2$ where W_o and W_t are the

Table 2. Intraspecific relationships between RNA concentration ($\mu g \cdot mg$ dry wt^{-1}) and individual dry weight, $[RNA] = aW^b$, of various zooplankton species. RNA concentration of an approximately average weight individual, $[RNA]_{\bar{W}}$, has been calculated by applying approximate average weight, $\bar{W} = (W_0 + W_t)/2$, to given regression equation. Average weights have been estimated from data given in: 1—Bakke 1977; Båmstedt and Matthews 1975; 2—Båmstedt 1976; 3—Jörgensen and Matthews 1975; Matthews and Hestad 1977; 4—Båmstedt 1978; Båmstedt unpubl.; 5—Matthews and Pinnoi 1973; Matthews and Hestad 1977.

		Regression equation					
	n	a	b	r^2	$\bar{W}$	Ref.	$[RNA]_{\bar{W}}$
Euchaeta norvegica ♀♀	119	12.01	−0.72	0.71	1.68	1	8.24
♂♂					0.75		14.83
Meganyctiphanes norvegica	119	36.54	−0.47	0.60	33.34	2	6.96
Thysanoessa sp.	5	27.75	−0.57	0.94	3.00	3	14.76
Boreomysis arctica	31	52.58	−0.76	0.72	7.50	4	11.38
Pasiphaea multidentata	12	22.84	−0.30	0.71	150.03	5	5.04
Parathemisto abyssorum	5	27.48	−0.19	0.40	4.00	4	21.13
Eukrohnia hamata	12	33.38	−0.71	0.67	2.50	4	17.39
Tomopteris helgolandica	5	69.89	−0.98	0.95	6.00	4	12.13
Aglantha digitale	6	10.07	−0.31	0.24	5.00	4	6.10

weights of juveniles and of adults, was estimated for each species and the corresponding RNA concentration calculated from the specific equation. Least-squares regression analysis indicated that 43% of the total interspecific variation in RNA concentration was explained by its correlation with dry weight. Since natural variability probably dominates in both variables and the population is open-ended, a geometric mean functional regression (Ricker 1973) was assumed to describe the relationship better (Fig. 4). The calculated regression equation is

$$[RNA] = 18.611 \times \bar{W}^{-0.315}.$$

Growth rate vs. dry weight—From the strict negative relationships between RNA concentration and body weight and the general inverse relationship between metabolic rate and body weight, it is clear that RNA concentration is positively correlated with metabolic activity and growth. The degree of correlation will determine the usefulness of estimating growth rates from measurements of RNA concentration. For comparison we have compiled published data on growth rate in relation to body weight. Growth rate is expressed as the coefficient of daily exponential growth, $k = (\ln W_t - \ln W_0)/t$ where W_0 and W_t are the initial and final weights for an interval of t days.

Intraspecific growth rate–dry weight relationships for nine species of zooplankton and two species of mesopelagic fish are shown in Fig. 5. Within a species the growth rate decreases quickly with increasing size (and age). The irregularities for some of the larger species (*Mysis relicta, Euphausia superba*) are due to decreased growth rates during winter—a common phenomenon for larger zooplankters at higher latitudes (Mauchline and Fisher 1969; Omori 1974; Jörgensen and Matthews 1975; Brinton 1976; Mauchline 1977).

Growth rates of zooplankton species from Korsfjorden and other (mostly temperate) areas are summarized in Table 3. The growth rate is calculated as the k value for the development from juvenile to adult. Since the growth rate of a species decreases markedly with increasing size, it is important for comparative purposes that the same segment of the life history is used when the average k is calculated. We have included only species for which data for most of the developmental period exist, but inevitably there is some variation, which is an additional source of variation in k. Besides body size, growth depends on many factors, such as temperature and food. We have chosen to include rather inhomogeneous data covering the size spectrum from copepods to small mesopelagic fishes, in order to have as wide as possible a scatter in the rela-

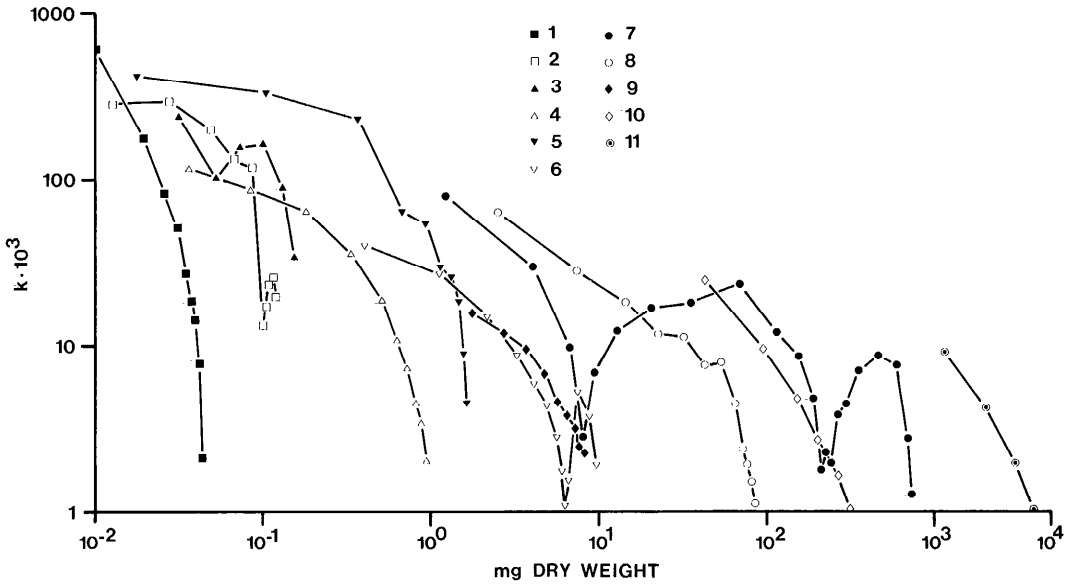

Fig. 5. Calculated relationships between growth rate and dry weight for nine species of zooplankton and two mesopelagic fishes. 1—*Daphnia pulex* (Richman 1958); 2—*Daphnia pulex obtusa* (Kryutchkova and Sládecek 1969); 3—*Lucifer chaecei* (Zimmerman 1973); 4—*Metamysidopsis elongata* (Clutter and Theilacker 1971); 5—*Artemia salina* (Reeve 1963); 6—*Mysis relicta* (Lasenby and Langford 1972); 7—*Euphausia superba* (Mackintosh 1972); 8—*Euphausia pacifica* (Smiles and Pearcy 1971); 9—*Sergestes similis* (Pearcy and Forss 1969); 10—*Maurolicus muelleri* (Gjösaeter 1978); 11—*Notoscopelus kroyeri* (Gjösaeter 1978).

tionship between RNA concentration and dry weight. For reasons given earlier, a geometric mean functional regression (Ricker 1973) was used to describe the interspecific relationship between average individual dry weight and growth rate (Fig. 6). The regression equation for all the data is

$$k \times 10^3 = 15.002 \times \bar{W}^{-0.317}.$$

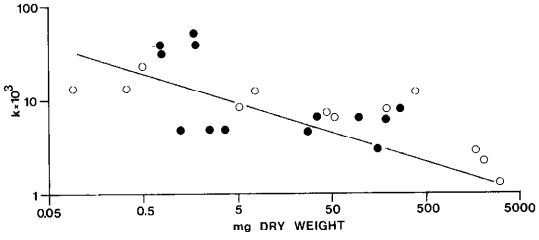

Fig. 6. Relationship (geometric mean functional regression) between coefficient of daily exponential growth (k) and average individual dry weight ($\bar{W}$) of zooplankton species from Korsfjord (●) and other areas (○). Regression equation: $k \times 10^3 = 15.002 \times \bar{W}^{-0.317}$. Further details given in Table 3.

Fenchel (1974) reviewed data on the intrinsic rate of natural increase, r_m, and found that this decreased with increasing individual size of the species. Over a weight range of 21 decades, the regression line describing this relationship on a double logarithmic diagram had a slope of −0.275. This is considerably less steep than the −0.32 for RNA vs. dry weight and k vs. dry weight in our study, suggesting that the tissue growth decreases faster than the net reproductive potential when going from species of smaller size to those of larger size.

RNA concentration vs. growth rate—For a given species the growth rate usually decreased faster with increasing size than explained by the interspecific relationship (cf. Figs. 5 and 6). The general trend of higher RNA concentrations in juveniles than in adults of similar size (Table 1, Fig. 3) is thus also reflected in the growth rate.

The interspecific relationships of RNA concentration and growth rate against dry

Table 3. Coefficients of daily exponential growth ($k \times 10^3$) for development period (t, days) from juvenile (weight = W_o) to adult (weight = W_t), $k = (\ln W_t - \ln W_o)/t$, for 9 zooplankton species from Korsfjord and 12 species from other areas. Average dry weight ($\bar{W}$) given as $(W_o + W_t)/2$.

	Dry wt (mg) $W_o - W_t$	t days	$k \times 10^3$	$\bar{W}$	References
		Korsfjorden			
Euchaeta norvegica					
♀, winter generation	0.017–3.30	100	52.7	1.66	Bakke 1977;
♂, winter generation	0.017–1.45	112	39.7	0.74	Båmstedt and Matthews 1975
♀, summer generation	0.017–3.40	134	39.5	1.71	
♂, summer generation	0.017–1.50	141	31.8	0.76	
Meganyctiphanes norvegica	5.80–60.87	365	6.5	33.34	Båmstedt 1976
Thysanoessa inermis	1.09–6.08	365	4.8	3.59	Jörgensen and Matthews 1975;
Thysanoessa raschii	0.73–4.08	365	4.8	2.41	Matthews and Hestad 1977
Thysanoessa longicaudata	0.37–2.09	365	4.8	1.23	
Nematoscelis megalops	8.99–46.07	365	4.5	27.53	
Sergestes arcticus ♀	28.38–489.42	365	7.9	258.90	Matthews and Pinnoi 1973;
S. arcticus ♂	35.26–326.87	365	6.2	181.07	Matthews and Hestad 1977
Pasiphaea multidentata	76.18–223.87	365	3.0	150.03	
Pasiphaea sivado	17.46–171.63	365	6.3	94.55	
		Other areas			
Euphausia pacifica	0.62–86.9	360	13.7	43.76	Smiles and Pearcy 1971
Euphausia superba	0.20–752.3	660	12.5	376.25	Mackintosh 1972
Thysanoessa raschii	0.002–15	705	12.5	7.50	Berkes 1976, 1977
Metamysidopsis elongata	0.024–0.97	159	23.2	0.49	Clutter and Theilacker 1971
Neomysis mirabilis	0.029–0.63	23	13.4	0.33	Shushkina 1972
Mysis relicta	0.179–10.06	474	8.5	5.12	Lasenby and Langford 1972
Lucifer chacei	0.017–0.165	17	13.4	0.09	Zimmerman 1973
Sergestes similis	13.7–93.9	300	6.4	53.80	Pearcy and Forss 1969
Sergestes lucens	6.6–369	450	8.9	187.80	Omori 1969
Notoscopelus kroyeri	774–5,376	1,460	1.3	3,075	Gjösaeter 1978
Maurolicus muelleri	1,222–2,088	1,022	2.8	1,655	Gjösaeter 1978
Benthosema glaciale	168–3,900	1,460	2.2	2,034	Gjösaeter 1978

weight (Figs. 4 and 6) had almost identical slopes (−0.315 and −0.317), suggesting a close correlation between specific growth rate and specific RNA concentration. The interspecific relationships were both based on values for mean-weight individuals, and one variable (dry weight) is therefore the same in the two equations. The dry weight can be expressed as a function (f_1) of RNA concentration. The growth coefficient ($k \times 10^3$) is a function (f_2) of the dry weight and can hence be expressed as a function (f) of RNA concentration. Thus

$$\bar{W} = f_1([\text{RNA}]);$$
$$k \times 10^3 = f_2(\bar{W});$$
$$k \times 10^3 = f_2\{f_1([\text{RNA}])\} = f([\text{RNA}]).$$

The actual data give the equations

$$\bar{W} = 10{,}617 \times [\text{RNA}]^{-3.171};$$
$$k \times 10^3 = 15.002 \times \bar{W}^{-0.317};$$
$$k \times 10^3 = 0.795 \times [\text{RNA}]^{1.004}.$$

Without losing much precision the last equation can be simplified to

$$k \times 10^3 = 0.795 \times [\text{RNA}].$$

Consideration of errors—The errors associated with estimating the growth rate of a mixed plankton sample from its average RNA concentration can be divided into five categories. 1. Methodological errors in the chemical analyses. 2. Inapplicability of the method for the types of organisms considered. 3. Error in the general growth rate–RNA relationship. 4. Variation in the growth rate–RNA relationship within and between species. 5. Error due to differences in biomass distribution between different species.

Although we did not thoroughly test every possible source of error in the analytical procedures, there is no reason to believe that this should bias the results markedly. With the development of fluo-

rimetric techniques (cf. Beers and Wittliff 1975), this source of error may be eliminated.

Errors of the second category are at present difficult to evaluate due to lack of data. The growth of phytoplankton can exceed $k = 10$ (Eppley 1972), and several microorganisms can reach values above $k = 50$ (Leick 1968). Obviously such high growth values cannot be derived from the equation presented above. Nongrowing animals do have some RNA present and the equation therefore does not give a realistic estimate in such a situation. The given k–RNA relationship should therefore be applied only to macrozooplankton samples and within the concentration range (3–70 μg RNA·mg dry wt^{-1}) for which it is described. As more information on the relationship between growth rate and RNA concentration of other types of organisms accumulates, we will find out whether a single general relationship is valid, or whether separate relationships for different groups of organisms must be applied.

The third type of error reflects the uncertainties in the RNA–dry weight and growth rate–dry weight relationships (Figs. 4 and 6) and can be reduced as more data become available.

The average growth rate of a mixed sample equals the product of specific growth rate and specific biomass summed over all species and divided by the total biomass in the sample. In the same way, the average RNA concentration can be derived from the specific RNA concentration and biomass. In practice the average RNA concentration of the mixed sample is measured and the corresponding growth coefficient is estimated by applying the general growth rate–RNA relationship. The degree of divergence from the real growth coefficient will be determined by the errors of the last two categories.

Any quantitative evaluation of the errors involved in the method must await further studies. Simultaneous measurement of growth rate and RNA concentration over whole life cycles of a variety of species from a broad size spectrum would provide the relevant information. From such information and from knowledge of the biomass distribution in the sample, correction terms could be added to the general equation, thereby increasing the accuracy in the estimate of growth rate.

References

BAKKE, J. L. 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**: 49–56.

———, AND N. J. SANDS. 1977. Hydrographical studies of Korsfjorden, western Norway, in the period 1972–1977. Sarsia **63**: 7–16.

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.

———. 1978. Studies on the deep-water pelagic community of Korsfjorden, western Norway. Seasonal variation in the weight and biochemical composition of *Chiridius armatus* (Copepoda), *Boreomysis arctica* (Mysidacea), and *Eukrohnia hamata* (Chaetognatha) in relation to their biology. Sarsia **63**: 145–154.

———, AND J. B. MATTHEWS. 1975. Studies on the deep-water pelagic community of Korsfjorden, western Norway. The weight and biochemical composition of *Euchaeta norvegica* Boeck in relation to its life cycle. Proc. 9th European Mar. Biol. Symp., p. 311–327. Aberdeen Univ.

———, AND H. R. SKJOLDAL. 1976. Studies on the deep-water pelagic community of Korsfjorden, western Norway. Adenosine phosphates and nucleic acids in *Euchaeta norvegica* (Copepoda) in relation to its life cycle. Sarsia **60**: 63–80.

BARNES, H., M. BARNES, AND D. M. FINLAYSON. 1963. The seasonal changes in body weight, biochemical composition, and oxygen uptake of the two common boreoarctic cirripedes, *Balanus balanoides* and *B. balanus*. J. Mar. Biol. Assoc. U.K. **43**: 185–211.

BAUDOUIN, M.-F., AND P. SCOPPA. 1975. The determination of nucleic acids in freshwater plankton and its ecological implications. Freshwater Biol. **5**: 115–120.

BEERS, P. C., AND J. L. WITTLIFF. 1975. Measurements of DNA and RNA in mammary gland homogenates by the ethidium bromide technique. Anal. Biochem. **63**: 433–441.

BERKES, F. 1976. Ecology of euphausiids in the Gulf of St. Lawrence. J. Fish. Res. Bd. Can. **33**: 1894–1905.

———. 1977. Production of the euphausiid crustacean *Thysanoessa raschii* in the Gulf of St. Lawrence. J. Fish. Res. Bd. Can. **34**: 443–446.

BRINTON, E. 1976. Population biology of *Euphau-*

sia pacifica off southern California. Fish. Bull. **74:** 733–762.

CHANDRAN, M. R., AND R. G. MICHAEL. 1968. The ribonucleic acid content in the marine amphipod *Talorchestia martensii*. Comp. Biochem. Physiol. **27:** 371–375.

CHURCH, R. B., AND F. W. ROBERTSON. 1966. A biochemical study of the growth of *Drosophila melanogaster*. J. Exp. Zool. **162:** 337–352.

CLUTTER, R. I., AND G. H. THEILACKER. 1971. Ecological efficiency of a pelagic mysid shrimp: Estimates from growth, energy budget, and mortality studies. Fish. Bull. **69:** 93–115.

DAGG, M. J., AND J. L. LITTLEPAGE. 1972. Relationships between growth rate and RNA, DNA, protein and dry weight in *Artemia salina* and *Euchaeta elongata*. Mar. Biol. **17:** 162–170.

DEVI, A., A. LEMONDE, U. SRIVASTAVA, AND N. K. SARKAR. 1963. Nucleic acids and protein metabolism in *Tribolium confusum* Duval. I. The variation of nucleic acid and nucleotide concentration in *Tribolium confusum* in relation to different stages of its life cycle. Exp. Cell Res. **29:** 443–450.

EPPLEY, R. W. 1972. Temperature and phytoplankton growth in the sea. Fish. Bull. **70:** 1063–1085.

FENCHEL, T. 1974. Intrinsic rate of natural increase: The relationship with body size. Oecologia **14:** 317–326.

GJÖSAETER, J. 1978. Resource studies of mesopelagic fish. Ph.D. thesis, Univ. Bergen.

JÖRGENSEN, G., AND J. B. 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.

KRYUTCHKOVA, N. M., AND V. SLÁDECEK. 1969. Quantitative relations of the feeding and growth of *Daphnia pulex obtusa* (Kurz) Scourfield. Hydrobiologia **33:** 47–64.

LANG, C. A., H. Y. LAU, AND D. J. JEFFERSON. 1965. Protein and nucleic acid changes during growth and aging in the mosquito. Biochem. J. **95:** 372–377.

LASENBY, D. C., AND R. R. LANGFORD. 1972. Growth, life history, and respiration of *Mysis relicta* in an arctic and temperate lake. J. Fish. Res. Bd. Can. **29:** 1701–1708.

LEICK, V. 1968. Ratios between contents of DNA, RNA and protein in different micro-organisms as a function of maximal growth rate. Nature **217:** 1153–1155.

LOWRY, O. H., N. J. ROSEBROUGH, A. L. FARR, AND R. J. RANDALL. 1951. Protein measurement with the Folin phenol reagent. J. Biol. Chem. **193:** 265–275.

MACKINTOSH, N. A. 1972. Life cycle of antarctic krill in relation to ice and water conditions. Discovery Rep. **36:** 1–94.

MATTHEWS, J. B., AND J. L. BAKKE. 1977. Ecological studies on the deep-water pelagic community of Korsfjorden (western Norway). The search for a trophic pattern. Helgol. Wiss. Meeresunters. **30:** 47–61.

———, 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.

———, AND S. PINNOI. 1973. Ecological studies on the deep-water pelagic community of Korsfjorden, western Norway. The species of *Pasiphaea* and *Sergestes* (Crustacea, Decapoda) recorded in 1968 and 1969. Sarsia **52:** 123–144.

MAUCHLINE, J. 1977. Growth and moulting of Crustacea, especially euphausiids, p. 401–422. *In* N. R. Andersen and B. J. Zahuranec [eds.], Oceanic sound scattering prediction. Plenum.

———, AND L. R. FISHER. 1969. The biology of euphausiids. Adv. Mar. Biol. **7:** 454 p.

MUNRO, H. N., AND E. D. DOWNIE. 1964. Relationship of liver composition to intensity of protein metabolism in different mammals. Nature **203:** 603–604.

———, AND A. FLECK. 1966. The determination of nucleic acids, p. 113–176. *In* D. Glick [ed.], Methods of biochemical analysis, v. 14. Wiley-Interscience.

———, AND J. A. GRAY. 1969. The nucleic acid content of skeletal muscle and liver in mammals of different body size. Comp. Biochem. Physiol. **28:** 897–905.

OMORI, M. 1969. The biology of a sergestid shrimp *Sergestes lucens* Hansen. Bull. Ocean Res. Inst. Univ. Tokyo **4:** 1–83.

———. 1974. The biology of pelagic shrimps in the ocean. Adv. Mar. Biol. **12:** 233–324.

PEARCY, W. G., AND C. A. FORSS. 1969. The oceanic shrimp *Sergestes similis* off the Oregon coast. Limnol. Ocenaogr. **14:** 755–765.

PEASE, A. K. 1968. The use of the estimates of ribonucleic acid to predict growth rates of zooplankton organisms. M.S. thesis, Univ. British Columbia. 107 p.

REEVE, M. R. 1963. Growth efficiency in *Artemia* under laboratory conditions. Biol. Bull. **125:** 133–145.

REGNAULT, M., AND P. LUQUET. 1974. Study by evolution of nucleic acid content of prepuberal growth in the shrimp *Crangon vulgaris*. Mar. Biol. **25:** 291–298.

RICHMAN, S. 1958. The transformation of energy by *Daphnia pulex*. Ecol. Monogr. **28:** 273–291.

RICKER, W. E. 1973. Linear regression in fishery research. J. Fish. Res. Bd. Can. **30:** 409–434.

SHUSHKINA, E. A. 1972. Intensity of production and utilization of assimilated food for growth of mysids from the sea of Japan. Oceanology **12:** 275–285.

SKJOLDAL, H. R., AND U. BÅMSTEDT. 1976. Studies on the deep-water pelagic community of Korsfjorden, western Norway. Adenosine phosphates and nucleic acids in *Meganyctiphanes norvegica* (Euphausiacea) in relation to its life cycle. Sarsia **61:** 1–14.

SMILES, M. C., JR., AND W. G. PEARCY. 1971. Size structure and growth rate of *Euphausia pacifica* off the Oregon coast. Fish. Bull. **69:** 79–86.

SULKIN, S. D., R. P. MORGAN, AND L. L. MINASIAN,

JR. 1975. Biochemical changes during larval development of the xanthid crab *Rhithropanopeus harrisii*. 2. Nucleic acids. Mar. Biol. **32:** 113–117.

SUTCLIFFE, W. H., JR. 1965. Growth estimates from ribonucleic acid content in some small organisms. Limnol. Oceanogr. **10**(suppl.): R253–R258.

———. 1970. Relationship between growth rate and ribonucleic acid concentration in some invertebrates. J. Fish. Res. Bd. Can. **27:** 606–609.

VICKERS, D. H., AND N. MITLIN. 1966. Changes in nucleic acid content of the boll weevil *Anthonomus grandis* Boheman during its development. Physiol. Zool. **39:** 70–76.

ZIMMERMAN, S. T. 1973. The transformation of energy by *Lucifer chacei* (Crustacea, Decapoda). Pac. Sci. **27:** 247–259.

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