GROWTH EFFICIENCY IN ARTEMIA UNDER LABORATORY CONDITIONS

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Measurements of the efficiency with which animals can convert food into their own body tissue have been largely confined to the vertebrates of agricultural importance. Typical of the wealth of data in Brody (1945) are figures for milk production in cows of 33%, egg production in hens of 10%, and for Jersey cows from 0 to 2 years an efficiency decrease from 35% to 5%. Ricker (1946) quoted a decrease from 33% to 10% with increasing age for fish, and Ivlev (1939a) found a value of 31% for young carp. Within the invertebrates Ivlev (1939b) also recorded an efficiency of 32% for young *Tubifex*, Fox *et al.* (1948) 0.9% for the marine worm, *Thoracophelia mucronata*, and North (1954) 11% for *Littorina*. Richman (1958), using four different feeding levels on three different ages of *Daphnia*, found efficiencies in the adult from 17% to 10% for food levels of 25 to 100 cells/mm.^{3} (*Chlorella*), respectively. Gibor (1957), feeding young *Artemia* on *Dunaliella*, reported a 53% efficiency, and Lasker (1960), feeding the same genus to *Euphausia*, found a variation between 11% and 74%. Conover (1961) obtained values around 15% for *Calanus hyperboreus* IV and V feeding on *Thalassiosira*.

Little work so far has been undertaken on the many factors which might influence growth efficiency in an invertebrate. The work reported below is an attempt to monitor weight increase and food consumption of groups of animals, both throughout their life cycle, and in greater detail over a limited period of their growth.

Materials and Methods

Dried eggs of *Artemia salina* (L.) were obtained from the Great Salt Lake, Utah. The alga, *Phaeodactylum tricornutum* Bohlin, originally sub-cultured from the Plymouth Marine Laboratory strain, had been maintained at Southampton for several years. The culture thrived in sea water, enriched only with inorganic nitrate and phosphate (Raymont and Adams, 1958). The sea water had a salinity of 35‰, and was filtered through two thicknesses of Whatman No. 1 paper and sterilized at 75° C.

The relationship between dry weight and length (from the anterior tip of the head to the base of the caudal furcae, following Gilchrist, 1959) was determined for *Artemia*, using nearly 80 separate samples at different ages. After being measured, the animals were rapidly washed in distilled water and oven-dried at 60° C. for three days. A torsion microbalance of the author's own design (Reeve, 1962) facilitated accurate weight determinations upon the smallest animals.

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In the first series of experiments, *Artemia* eggs were hatched and the nauplii kept without food for 36 hours while they used up their yolk reserves. Four batches of 100 nauplii (A, B, C and D) were then put in vessels in 50 ml. of culture medium at concentrations of 100, 75, 50 and 25 *Phaeodactylum* cells/mm.^{3}, respectively. A fifth vessel contained culture medium at a known concentration, but was without animals. This was to serve as a control to determine whether the plant cells were multiplying or sinking out of suspension. All five vessels were placed overnight in a dark cupboard at 20 ± 1° C. On the following day, a sample of liquid was withdrawn from each vessel, and its cell concentration counted with the aid of a Sedgewick-Rafter chamber. At the same time, all the animals were transferred from the vessels containing them to dishes, and all the vessels were re-filled with fresh medium at the original cell concentrations. The number of animals remaining alive was recorded and they were replaced in their respective vessels, which were then returned to the dark cupboard. This cycle of events was repeated daily.

The increase in feeding capacity of the animals, as measured by their depletion of the food cells each day, was such that the volume of their medium had to be progressively increased. By the time sexual maturity was reached, about five pairs of animals (male and female) remained in each experiment, and occupied 3000 ml. At this time there were from 30 to 60 survivors of the original 100, but it was necessary to reduce this number to avoid the handling of excessive volumes of sea water. The mature animals started mating and produced nauplii, which were counted and removed from the water daily. The experiments were brought to a conclusion after 55 days.

The cell counting technique consisted in taking ten random fields of the Sedgewick-Rafter chamber. The reliability of the mean of ten counts was estimated (Reeve, 1962) at ±10–15% at the 95% confidence level. Counts of the control suspension very rarely varied significantly in density over 24 hours.

The second series of experiments were undertaken to gather some information on the effects of the variation of temperature, salinity, and a greater range of food concentration on growth efficiency. It was decided, in order to restrict the work involved, to use animals over a limited period of their life cycle. Young animals, which had just used up their yolk reserves, were chosen. This ensured that all experiments began with animals in an equivalent physiological condition. The sex, phase of sexual cycle, and genetical differences between individuals, all exert progressively greater effects on feeding rates in *Artemia* as it gets older (Reeve, 1962).

Arbitrary standards of temperature, salinity, and food concentration were set at 20° C., 35‰, and 50 cells/mm.^{3}, respectively. Three groups of experiments were performed, in which one of these parameters was varied while the other two were held constant. Eggs were hatched in a medium of the same temperature and salinity as their respective experiments. The effect of temperature on growth efficiency in young *Artemia* was investigated using six temperatures ranging from 5° to 30° C. A series of salinities from 5‰ to 150‰ were employed in the salinity variation experiments. These were obtained by evaporating sea water at 75° C., and then diluting the concentrated brine as required. Six food cell concentrations from 5 to 200 cells/mm.^{3} were chosen to determine the effect of food concentration on growth efficiency.

TABLE I

Cumulative length, weight and number of offspring of animals; and number and weight of plant cells consumed and growth efficiency, in five-day intervals for experiments A–D. (Weight at birth has been taken into account in computing efficiency)

Exp.	Interval (days)	Length (mm.)	Number of young	Wt. animals + young (mg.)	No. cells eaten $\times 10^{-3}$	Wt. cells eaten (mg.)	Efficiency (%)
	5	1.35		0.0040	613	0.0066	30
	10	3.30		0.0323	7,690	0.0830	39
	15	5.70		0.174	43,200	0.467	37
	20	8.50		0.575	121,000	1.31	44
	25	9.60	26	0.896	225,000	2.43	37
A	30	10.60	113	1.40	347,000	3.75	37
	35	11.20	156	1.71	471,000	5.09	34
	40	11.75	198	2.01	588,000	6.35	32
	45	12.15	240	2.30	744,000	8.04	29
	50	12.35	339	2.63	932,000	10.1	26
	55	12.45	477	2.94	1,039,000	11.2	26
	5	1.40		0.0039	589	0.0064	30
	10	3.60		0.0427	6,280	0.0678	60
	15	5.45		0.148	24,700	0.267	55
	20	8.10		0.501	76,900	0.831	60
	25	9.20	11	0.752	148,000	1.60	47
B	30	9.90	62	1.07	236,000	2.55	42
	35	10.40	122	1.36	324,000	3.50	39
	40	10.80	146	1.55	409,000	4.42	35
	45	11.00	171	1.66	500,000	5.40	31
	50	11.10	223	1.83	596,000	6.44	28
	55	11.15	302	2.05	661,000	7.14	29
	5	1.20		0.0032	401	0.0043	28
	10	2.25		0.0105	3,010	0.0325	26
	15	4.15		0.0661	13,300	0.144	45
	20	6.10		0.210	34,100	0.368	57
	25	8.50		0.575	74,000	0.799	72
C	30	9.30	17	0.802	129,000	1.39	58
	35	9.80	28	0.939	174,000	1.88	50
	40	10.15	50	1.09	246,000	2.66	41
	45	10.40	91	1.27	338,000	3.65	35
	50	10.50	116	1.38	402,000	4.34	32
	55	10.55	182	1.56	517,000	5.58	28
	5	1.00		0.0029	201	0.0022	41
	10	1.90		0.0063	916	0.0099	43
	15	3.00		0.0246	3,790	0.0410	55
	20	4.60		0.912	10,800	0.117	76
	25	6.15		0.219	25,500	0.275	79
D	30	7.50		0.398	47,900	0.520	76
	35	8.30	9	0.546	75,200	0.812	67
	40	8.90	9	0.683	99,100	1.07	64
	45	9.15	35	0.811	133,000	1.44	56
	50	9.20	59	0.881	187,000	2.02	44
	55	9.20	100	0.984	224,000	2.42	41

The experiments began with 100 animals and proceeded as detailed for the first series, with regard to daily maintenance. They were concluded as the average length of the animals reached approximately 2 mm., which occurred within five days for those under the standard conditions. By the eleventh day, animals in all the experiments had attained this size, except those at 5° and 10° C. These two were growing so slowly that they were also discontinued on the eleventh day. Samples of about 15 animals were weighed at the end of each experiment, using the torsion microbalance. In this way, any weight increase could be directly determined, rather than having to rely on a length/weight relationship.

Results

The efficiency of growth of *Artemia* $\left(\frac{\text{wt. of animal produced}}{\text{wt. of plant consumed}}\right)$ was computed for the first series of experiments in the following manner (see Table I). The 55-day period was divided into 11 successive 5-day units. Average values were extracted from the data for animal length, number of offspring, and number of *Phaeodactylum* cells consumed per animal to the end of each period. The first two quantities were transformed to estimations of dry weight, using the weight/length relationship. This was represented by a straight line (Fig. 1) over most of its length when plotted on double logarithmic coordinates. Cell numbers were related to dry weight, using the data of Raymont and Adams (1958), who found a million cells of this species weighed 0.0108 mg. The efficiency to the end of each period, or cumulative efficiency, in the four food concentrations could then be derived as in the last column of Table I. Figure 2 A–D (corresponding to experiments A–D) is a graphical representation, in which the growth rate curve for each experiment (as increase in length) has also been included.

It is clear that there is a definite peak efficiency which occurs about the time of inflexion of the growth rate curve. The peak is highest in the lowest food levels, although the rate of growth is slower, the onset of sexual maturity is later, and the broods and the ultimate size of the animals are smaller. Table I contains cumulative efficiencies up to the end of each successive five-day period. Efficiencies within each period, or moving efficiencies, may also be extracted by simple calculation, from this table. These indicate the actual efficiency level at which the food conversion process is working during the five-day period under consideration. A plot of moving efficiencies would follow those of cumulative efficiencies in Figure 2 fairly closely. This is because the progressively greater quantities involved, as the animals grow and eat more, tend to swamp the earlier smaller figures, and minimize the cumulative effect. One of the main discrepancies is to be found in the peak values, which, considered by themselves (without the cumulative effect of the previous values), would be up to 10% higher. The other is in the latter parts of the curves, which in Figure 2 are falling to values between 25% and 40%. The moving efficiencies would tend to level off to values of 15–25%. Stability is achieved because the animals have become relatively fixed in size, feeding rate, and reproductive capacity. This 15–25% could be called the "reproductive efficiency," or efficiency of production of offspring, and is highest in the lowest food concentrations, though the numbers of young produced are much lower.

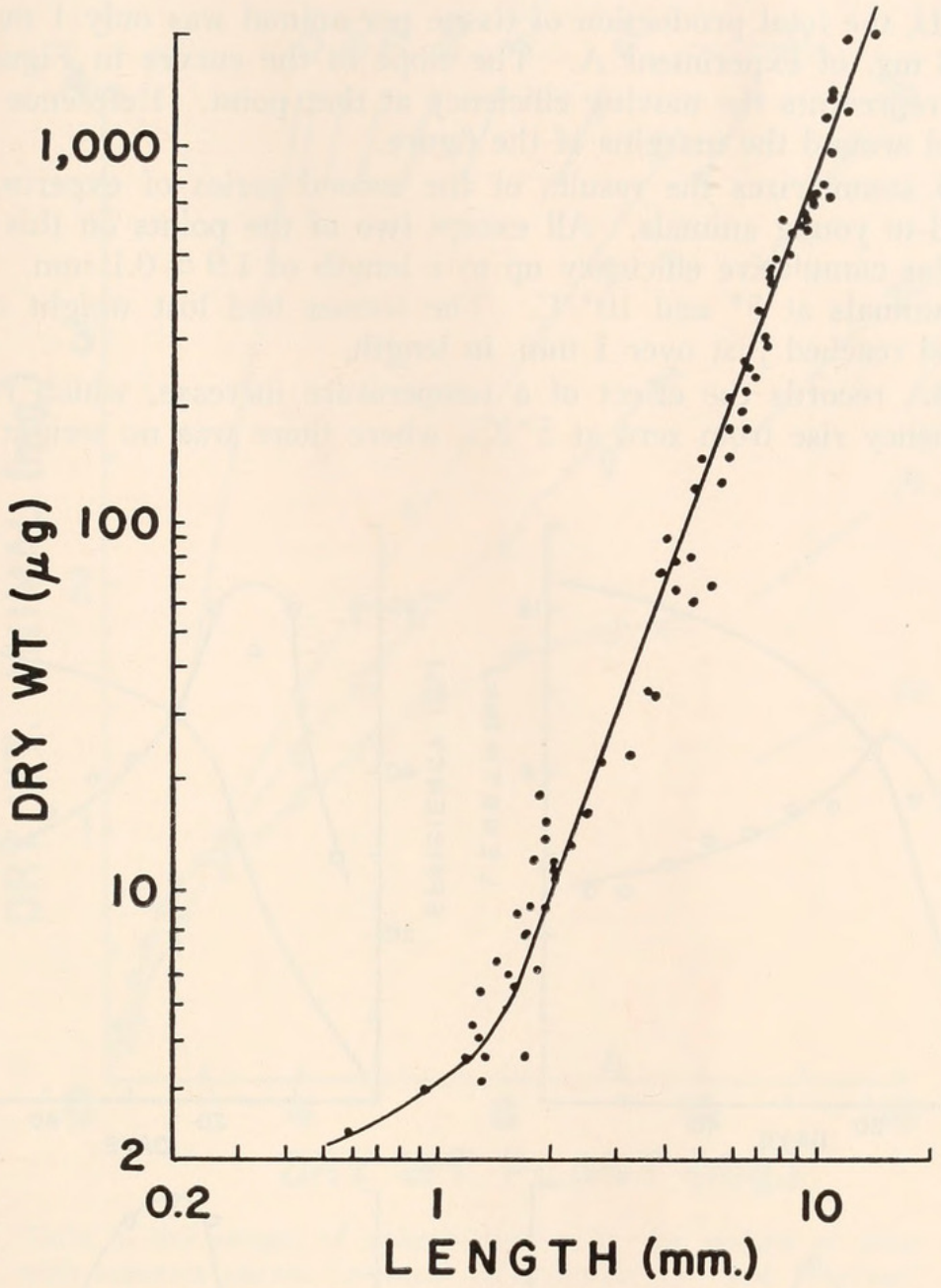


FIGURE 1. Weight/length relationship in *Artemia*.

These efficiency figures are average values. As the male animal reaches its maximum size and its rate of weight increase approaches zero, it continues to consume food. However, as this is used exclusively for non-tissue-forming metabolic functions, its growth efficiency also approaches zero. The female continues to use much of her food for the production of young, even after she has ceased to grow, and so maintains a high efficiency. Figure 2 assumes an "average" male/female animal, but in Figure 3 this average is separated into its male and female elements for experiment A. This is an alternative method of expressing the results, as weight of animal tissue produced against weight of plants consumed. Figure 3 is less sensitive than Figure 2 in demonstrating changes in efficiency during the earlier part of the life cycle of the animals. This is clear from the "average" curve for experiment D, which has also been inserted in Figure 3. This Figure is, however, useful in comparing the overall production of animal tissue in the two experiments. Although the food conversion process was more efficient in

experiment D, the total production of tissue per animal was only 1 mg. compared with the 2.8 mg. of experiment A. The slope of the curves in Figure 3 at any given point represents the moving efficiency at that point. Reference slopes have been inserted around the margins of the figure.

Figure 4 summarizes the results of the second series of experiments, which was confined to young animals. All except two of the points on this figure indicate values for cumulative efficiency up to a length of 1.9 ± 0.1 mm. The exceptions were animals at 5° and 10° C. The former had lost weight slightly, and the latter had reached just over 1 mm. in length.

Figure 4A records the effect of a temperature increase, which resulted in a growth efficiency rise from zero at 5° C., where there was no weight gain, up to

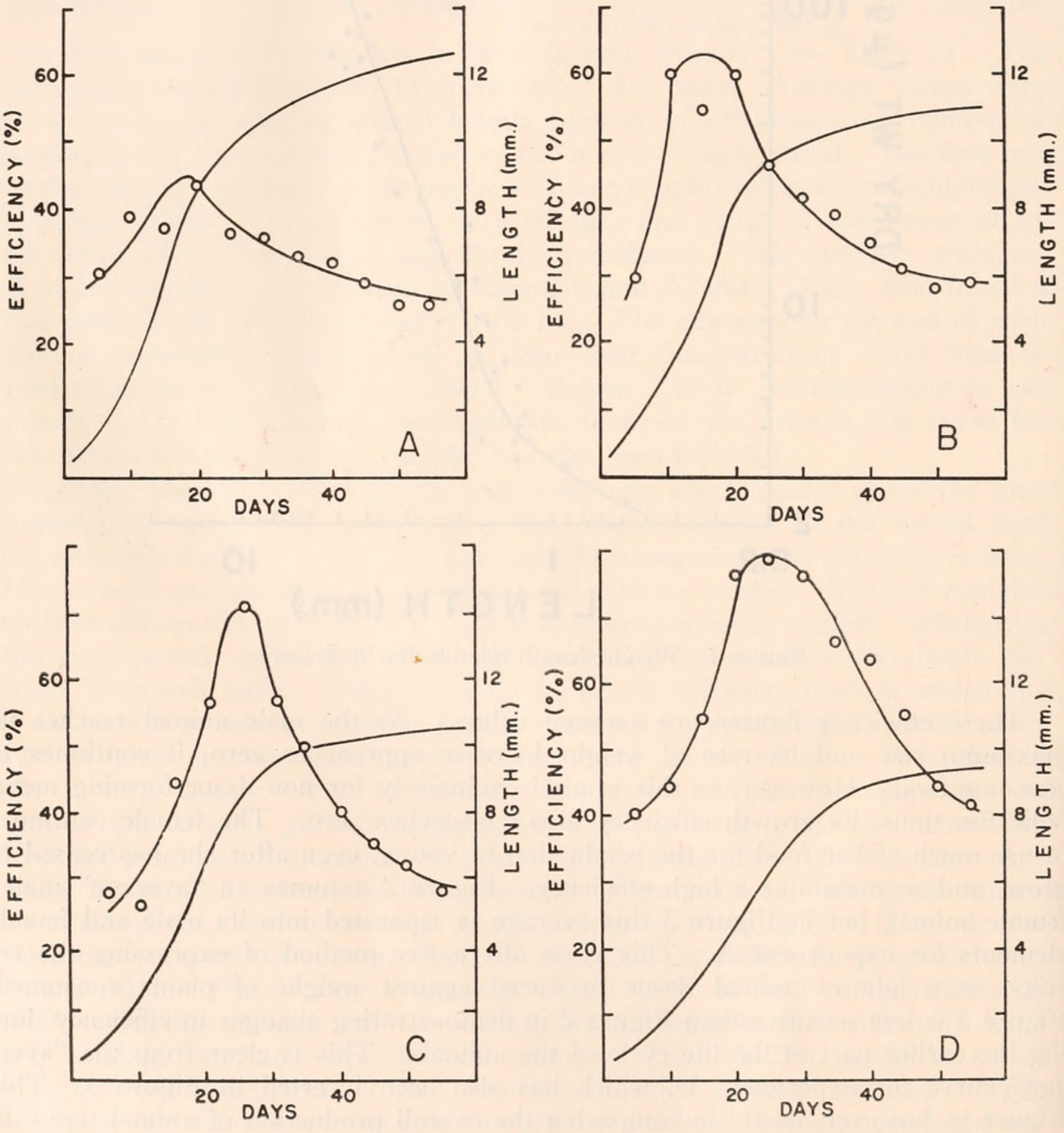


FIGURE 2. Cumulative efficiency (circles) and increase in length for experiments A–D.

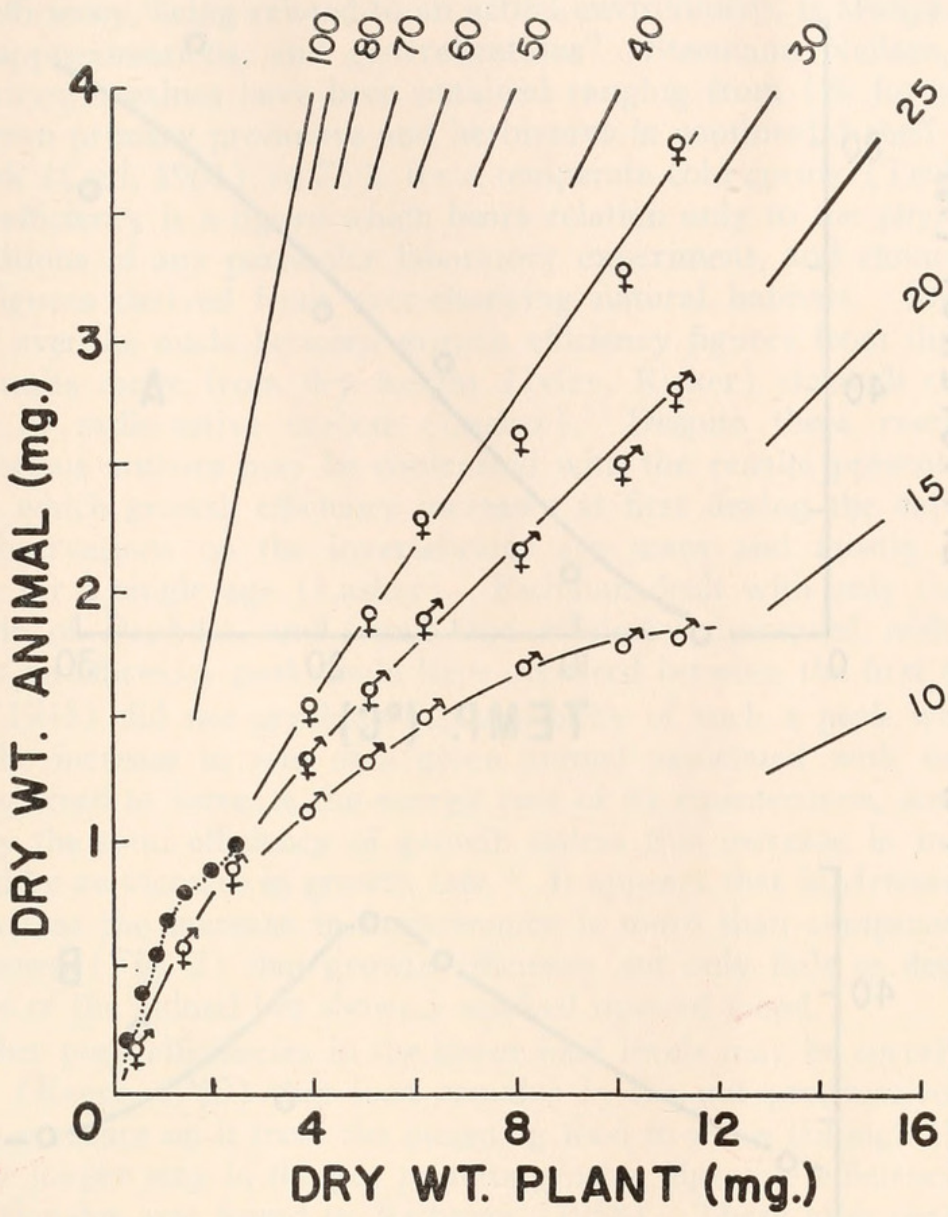
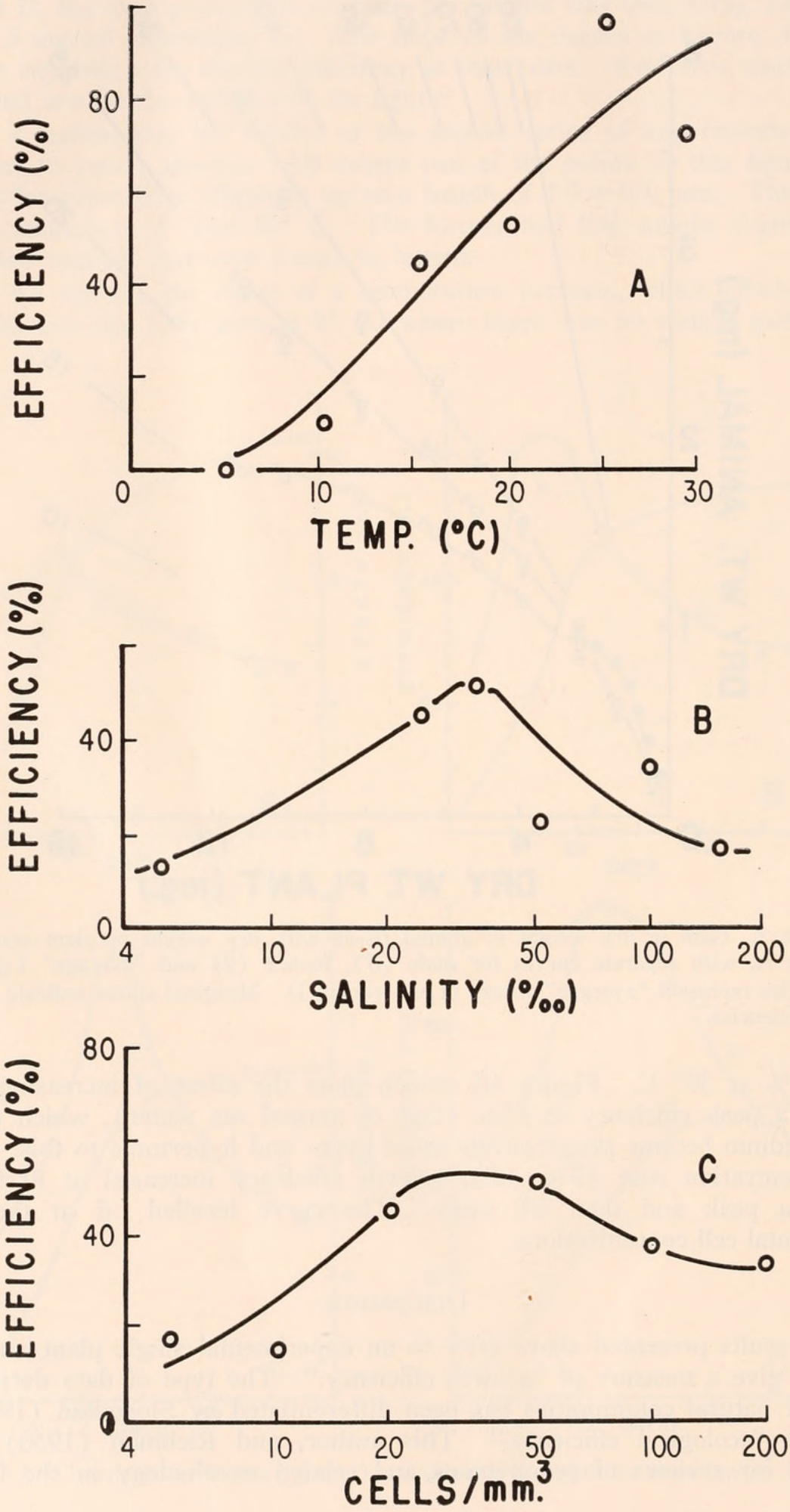


FIGURE 3. Gain in dry weight of animal tissue with dry weight of plant consumed for experiment A, with separate curves for male (♂), female (♀) and "average" (⚥) animal. Closed circles represent "average" animal of experiment D. Marginal slopes indicate percentage moving efficiencies.

about 85% at 30° C. Figure 4B, which plots the effect of increasing salinity, suggests a peak efficiency at 35‰ (that of normal sea water), which decreased as the medium became progressively more hypo- and hypertonic to this. As food cell concentration rose (Fig. 4C), growth efficiency increased at first rapidly, reached a peak and then fell away. The curve levelled off at the highest experimental cell concentrations.

DISCUSSION

The results presented above refer to an experimental single plant/animal system, and give a measure of "growth efficiency." The type of data derived from studies of natural communities has been differentiated by Slobodkin (1960) with the name "ecological efficiency." This author, and Richman (1958) may be consulted for reviews of synonymous and related terminology in the literature.


EFFICIENCY (%)
80
40
0
A
0
10
20
30
TEMP. (°C)
EFFICIENCY (%)
40
0
B
4
10
20
50
100
200
SALINITY (‰)
EFFICIENCY (%)
80
40
0
C
4
10
20
50
100
200
CELLS/mm.3

Ecological efficiency, being related to an actual environment, is always the result of "averages, approximations, and generalizations" (Steemann Neilsen, 1961). In ecological surveys, values have been obtained ranging from 1% for conversion of carbon between primary producers and herbivores in continental shelf waters south of New York (Curl, 1961), to 75% for a temperate cold spring (Teal, 1957).

Growth efficiency is a figure which bears relation only to the physical and biological conditions of any particular laboratory experiment, and cannot be directly related to figures derived from ever-changing natural habitats. Strict comparisons cannot even be made between growth efficiency figures from different workers, where units range from dry weight (Ivlev, Ricker) through calorific value (Richman) to radio-active carbon (Lasker). Despite these reservations, the work of previous authors may be contrasted with the results presented above for *Artemia,* in which growth efficiency increases at first during the early life of the animal. Observations on the invertebrates are scant and mostly single values (Gibor), or for a single age (Lasker). Richman dealt with only three points in the life cycle of *Daphnia,* and found that efficiency decreased with age. It is possible that an efficiency peak could have occurred between the first two points.

Brody (1945) did not preclude the possibility of such a peak when he stated (p. 49), "the increase in size of a given animal associated with increasing age would be expected to increase the energy cost of its maintenance, and reduce correspondingly the total efficiency of growth unless this increase in maintenance is compensated by an increase in growth rate." It appears that in *Artemia* the growth rate is such that the increase in maintenance is more than compensated, since it has been shown (Fig. 2) that growth efficiency not only fails to decrease during the early life of the animal but shows a marked upward trend.

The higher peak efficiencies in the lower food levels may be correlated with the observation (Reeve, 1962) that food remains in the gut progressively longer, as there is less pressure on it from the incoming food to move through the gut. Presumably, the longer stay in the gut permits greater digestive efficiency. A similar inverse relationship was found by Richman (1958). These high peak values may be compared with 73% for *Mytilus* veligers (Jørgensen, 1952), 16–74% for *Euphausia* (Lasker, 1960) and figures for pre-natal growth of embryos of hen, frog, fish and silkworm of 52%, 51%, 59% and 65%, respectively (Brody, 1945). These figures imply very high digestive efficiencies within the range that have been reported by Marshall and Orr (1955) for *Calanus,* Lasker (1960) for *Euphausia* and Berner (1962) for *Temora.* All three workers found values of over 90%. If *Artemia* is capable of assimilating such high percentages of its ingested food, then peak growth efficiencies of up to 80% are theoretically possible.

In order to measure directly the weight of animals as they grow, a sample of the population must be sacrificed at frequent intervals. To do this the population must be either inconveniently large, or the work must be restricted to a small part of the life-cycle. The former situation was avoided by using length as an index of weight in the first series of experiments; the second series was of short duration, and the animals were directly weighed at the conclusion of each experiment. The results of the second series may thus have been determined with greater accuracy,

FIGURE 4. Relationship between cumulative efficiency and (A) temperature, (B) salinity, and (C) food concentration in young animals.

since the intermediate stage of computation was eliminated. As before, efficiencies were computed in general over no less than a five-day period. It must be noted, however, that the figures so derived did not necessarily represent animals of equivalent physiological ages. Discrepancies were most marked in the lower temperature experiments, where animals did not grow enough to reach the length of 2 mm., arbitrarily set for the conclusion of each experiment. At 5° C., only one-third of the animals had passed through their first molt, and averaged no more than 0.5 mm. in length by the eleventh day.

Efficiency in young animals varies markedly with salinity, and there appears to be an optimum corresponding to normal sea water. This is further evidence that the brine shrimp is not physiologically adapted to high salinities, any more than it is by virtue of its ionic regulation mechanism (Croghan, 1958), which has such a wide tolerance range that the animal can exist in water down to 15% normal sea water. Though Potts (1954) computed that the proportion of the total work expended on maintaining osmotic equilibrium in reduced salinities is theoretically very small, Croghan (1961) pointed out that such minimal levels are not likely to occur in practice. The osmotic work involved in keeping an internal fluid hypotonic in strong brines is not known. It may be that the decrease in growth efficiency, in both hypo- and hypertonic sea water, is at least partly due to increased proportions of assimilated food being appropriated for osmotic work. Beament (1961) developed the hypothesis that physiological specialization is far less significant than behavioral specialization in restraining animals to particular environments. As others have suggested, it may be the inability of *Artemia* to defend itself from predation which is important in limiting its natural habitat to saline lakes.

Although *Artemia* has been shown to utilize its food more efficiently in lower cell concentrations, this trend must ultimately reverse and drop to zero. This would occur at the cell concentration when the food passing through the gut is sufficient to do no more than provide for maintenance, leaving nothing available for building new tissue. In young animals (Fig. 4C) this trend is evident, with a maximum growth efficiency occurring in a food level between 25 and 35 cells/mm.^{3}. At higher cell concentrations, efficiency falls as the food moves through the gut faster, until about 200 cells/mm.^{3} when it levels off. This cell concentration has been correlated in young animals (Reeve, 1963) with that at which a maximum rate of ingestion is reached, *i.e.*, in cell concentrations above this, food moves through the gut at the same constant rate.

In this work, precautions were taken to reduce any effect due to bacteria, by using sterilized water in both plant and animal cultures. The experimental media were changed daily, and the plant cultures were rejected at any sign of a bacterial buildup, and in any case were used only in their rapidly growing phase. However, the experiments were undoubtedly not completely bacteria-free, and hence all efficiencies will have been slightly overestimated. Antibiotics were not used to kill bacteria, as they were suspected to have a depressive influence on filtration rate in copepods (Conover *et al.*, 1959).

These feeding experiments serve to indicate several factors which can influence growth efficiency, even though they may be claimed only as preliminary in the field of continuous measurement throughout life of an invertebrate laboratory population. The combined effect of all the errors involved in these determinations cannot be

estimated with any accuracy. The insensitive logarithmic length/weight relationship used in the first series of experiments, and the small size of the young animals, would probably combine to render the earlier parts of the efficiency curves least accurate. For instance, the animals of experiment C, unlike the others, appear to have attained only 30% efficiency after 10 days of growth, although from Figure 4C of the second series, a value of about 50% was recorded in a comparable experiment. This is, in all probability, an extreme case. However, there is little doubt that efficiency peaks exist, and are related to food concentration and growth rate.

There have been several attempts to raise the productivity of natural aquatic environments by adding inorganic fertilizers, in order to obtain an eventual increase in the yield of animal tissue (*e.g.,* Gross *et al.,* 1950). By dependence on a transfer of energy through several links of the food chain, the results of these attempts have proved uneconomical and difficult to predict. Direct harvesting of mass cultures of algal cells (Burlew, 1953; Raymont and Adams, 1958) is also prohibitively expensive. Raymont (personal communication) suggested that experiments intermediate between these two extremes should be undertaken. A filter-feeding herbivore might be used to harvest the algal cells, because the animal would be relatively easy to remove from the environment. The work reported above indicates that the conversion of plant to animal tissue, could, by careful choice of conditions, be maintained at an efficiency well over 50%.

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Addendum

Since the preparation of this paper, Mason (1963) reported some feeding experiments with *Artemia,* which may be compared with those of this work. In this work the volume of the medium was adjusted often as the animals grew. This was to ensure, as far as possible, that the cell depletion over 24 hours exceeded that required for statistical significance, but was not more than 50% of the original concentration. Mason was concerned mainly with offering a constant specified number of food cells to his animals each day as they grew. Although some of his experiments were begun daily at a variety of food concentrations, he reported that the nauplii consumed up to 99% of the food in 24 hours. In the first series of experiments the growth of his animals was severely stunted by the lack of an adequate supply of food. Under such conditions no conclusions may be drawn concerning the effect of cell concentration upon growth rate. Under natural conditions it is generally the concentration, rather than the absolute amount of food in the environment, which is of importance to the filter-feeder from day to day. The very low growth efficiencies recorded by Mason may be partly a reflection of the fact that his animals were progressively more limited by their food supply. It may be pointed out that he finds higher efficiency values during the active growth phase of

Artemia. In short-term experiments with adult animals he obtained an average of 17% for growth efficiency. This is much closer to figures reported in the present work.

Summary

1. The efficiency of growth of four laboratory populations of *Artemia* in different food concentrations was studied over a period from birth to approximately double the time required to reach sexual maturity. Uptake of food and increase in length, and hence weight, were measured daily. Efficiency rose at first, up to the time at which the animals were growing at their maximum rate, when the highest peak cumulative efficiencies (79%) were obtained in the lowest food concentrations. These values then fell as the animals approached their maximum size.

2. In other experiments on young animals in their first few days of growth, it was found that efficiency increased with temperature between 5° and 30° C., that there was an optimum salinity of about 35‰, at which efficiency was greatest, and an optimum food concentration of 25–30 cells/mm.^{3}.

LITERATURE CITED

Beament, J. W. L., 1961. The role of physiology in adaptation and competition between animals. *Symp. Soc. Exp. Biol.*, **15**: 62–71.

Berner, A., 1962. Feeding and respiration in the copepod *Temora longicornis* (Müller). *J. Mar. Biol. Assoc.*, **42**: 625–640.

Brody, S., 1945. Bioenergetics and Growth. Reinhold Publishing Co., New York.

Burlew, J. S., 1953. Algal culture from laboratory to pilot plant. *Publ. Carnegie Institution*, **600**: 1–357.

Conover, R. J., 1961. Metabolism and growth in *Calanus hyperboreus* in relation to its life cycle. Zooplankton Production, Symposium, Cons. Int. Explor. Mer., unpublished paper no. 11.

Conover, R. J., S. M. Marshall and A. P. Orr, 1959. Feeding and excretion of *Calanus finmarchicus* with reference to the possible role of the zooplankton in the mineralization of organic matter. Unpublished manuscript, Woods Hole Oceanographic Institution, Ref. no. 59–32.

Croghan, P. C., 1958. The osmotic and ionic regulation of *Artemia salina* (L.). *J. Exp. Biol.*, **35**: 219–233.

Croghan, P. C., 1961. Competition and mechanisms of osmotic adaptation. *Symp. Soc. Exp. Biol.*, **15**: 156–167.

Curl, H., 1961. Standing crops of carbon, nitrogen, and phosphorus and transfer between trophic levels, in Continental Shelf waters south of New York. Zooplankton Production, Symposium, Cons. Int. Explor. Mer., unpublished paper no. 32.

Fox, D. L., S. C. Crane and B. H. McConnaughey, 1948. A biochemical study of the marine annelid worm, *Thoracophelia mucronata*, its food, biochromes and carotinoid metabolism. *J. Mar. Res.*, **7**: 567–585.

Gibor, A., 1957. Conversion of phytoplankton to zooplankton. *Nature*, **179**: 1304.

Gilchrist, B. M., 1959. The metabolism of *Artemia salina* (L.). Ph.D. Thesis, University of London.

Gross, F., S. R. Nutman, D. T. Gauld and J. E. G. Raymont, 1950. A fish cultivation experiment in an arm of a sea loch. I–V. *Proc. Roy. Soc. Edinb., Ser. B*, **64**: 1–135.

Ivlev, V. S., 1939a. Balance of energy in carps. *Zool. Zhurnal*, **18**: 303–318.

Ivlev, V. S., 1939b. Transformation of energy by aquatic animals. *Int. Rev. Hydrobiol.*, **38**: 449–458.

Jørgensen, C. B., 1952. Efficiency of growth in *Mytilus edulis* and two gastropod veligers. *Nature*, **170**: 714.

LASKER, R., 1960. Utilization of organic carbon by a marine crustacean: Analysis with Carbon-14. *Science,* **131**: 1098.

MASON, D. T., 1963. The growth response of *Artemia salina* (L.) to various feeding regimes. *Crustaceana,* **5**: 138–150.

MARSHALL, S. M., AND A. P. ORR, 1955. On the biology of *Calanus finmarchicus.* VIII. Food uptake, assimilation, and excretion in adult and stage V *Calanus. J. Mar. Biol. Assoc.,* **34**: 495–529.

NORTH, W. J., 1954. Size distribution, erosive activities, and gross metabolic efficiencies of the marine intertidal snails, *Littorina planaxis* and *L. scutulata. Biol. Bull.,* **106**: 185–197.

POTTS, W. T. W., 1954. The energetics of osmotic regulation in brackish and freshwater animals. *J. Exp. Biol.,* **31**: 618–630.

RAYMONT, J. E. G., AND M. N. E. ADAMS, 1958. Studies on the mass culture of *Phaeodactylum. Limnol. Oceanogr.,* **3**: 119–136.

REEVE, M. R., 1962. Quantitative aspects of feeding and food conversion in *Artemia salina* (L.). Ph.D. Thesis, University of Southampton.

REEVE, M. R., 1963. The feeding of Artemia I: In pure cell cultures. *J. Exp. Biol.,* **40**: 195–205.

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

RICKER, W. E., 1946. Production and utilization in fish populations. *Ecol. Monogr.,* **16**: 375–391.

SLOBODKIN, L. B., 1960. Ecological energy relationships at the population level. *Amer. Nat.,* **94**: 213–236.

STEEMANN NEILSEN, E., 1961. The relationship between phytoplankton and zooplankton in the sea. Plankton Production, Symposium, Cons. Int. Explor. Mer., unpublished paper no. 4.

TEAL, J. M., 1957. Community metabolism in a temperate cold spring. *Ecol. Monogr.,* **27**: 283–302.